Bulletin of the Museum of Comparative Zoölogy

AT HARVARD COLLEGE

VOL. 105, No. 2

COMPARATIVE GENITAL ANATOMY OF SOME AFRICAN ACHATINIDAE (PULMONATA)

BY ALBERT R. MEAD

WITH NINE PLATES

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
December, 1950

No. 2. — *Comparative Genital Anatomy of Some African Achatinidae (Pulmonata)*[1]

By Albert R. Mead
Department of Zoology
University of Arizona

CONTENTS

[1] Published with the aid of a grant from the Pacific Science Board of the National Research Council, Washington, D. C.

When this is once determined, it is usually not very difficult to make a correct identification even when the specimen is rather poorly preserved. Too often, though, a specimen such as this latter is used in setting forth the details of the genital anatomy. This is especially perilous where uniques are involved.

No matter what method is used in killing snails, there is always danger of producing at least a small amount of distortion in the genital system. Preserving in formalin after insufficient drowning will cause the animal to contract to such an extent that severe distortion of the soft parts will inevitably result. In addition, the acid in the formalin will not only attack the shell but will also dissolve the cementing substance that makes the periostracum adhere to the shell. Treatment with alcohol, under similar conditions is just as bad, as the dehydration will alter the general proportions, shrink the tissues and make the specimen hard enough so that it will be difficult to examine. Drowning to such an extent that there is little or no contraction when the specimen is immersed in a preservative still does not get away from distortion as the dead and dying tissues take on a great deal of water and thereby assume unnatural proportions.

Preserving the animal in formalin or alcohol while it is still in its shell, even under the best conditions, will create a real problem when attempts are made later to remove the soft parts without damaging or destroying completely the shell. A tearing of the visceral mass in its central portions is the usual result. Prolonged soaking in water or various solutions seldom is of any avail. Boiling will invariably cause it to shrink so badly that it is worthless as a scientific specimen.

The author has found that by far the best method is to plunge the partially drowned specimen into rapidly boiling water and examine it as soon as the columellar muscle has loosened sufficiently to permit extraction of the soft parts. This not only leaves the genitalia still very flexible but their immediate removal obviates the danger of making permanent any distortion due to the crowding effects of contraction. Added advantages are found in the ease with which the soft parts can be removed and in the undamaged shell specimen that remains. Too sudden cooling of the shell, however, may cause the periostracum to crack and flake off; the shell is therefore usually reimmersed in the hot water, after the soft parts are removed, and allowed to undergo gradual temperature changes as the water cools.

The soft parts, including the removed genitalia, are preserved in 6% formalin solution, as 70% alcohol dehydrates and shrinks the tissues and needs replenishing too often. Specimens that have become brittle with preservation in alcohol and even specimens that have been allowed to dry out completely have been restored to nearly

natural proportions and a most remarkable degree of flexibility through the use of an 0.8% solution of trisodium phosphate as recommended by Van Cleave and Ross (1947). Such specimens, whether genitalia or the entire snail, were soaked from a few hours to several days with never the slightest suggestion of maceration or distortion even in the longer period of time.

During the months of May and June, 1948, F. X. Williams, entomologist of the Hawaiian Sugar Planters' Association, sent, under special permission, live specimens of several species of the genus *Achatina* from Kenya Colony and Zanzibar. There is indeed little doubt that this is the largest shipment of live achatinas ever to be shipped to this country, and perhaps the western hemisphere. These formed the bulk of the live material examined in this study. The rest of the live material was collected in the Gold Coast and Nigeria by the author while on duty as Parasitologist of the Inter-Allied Malaria Control unit in British West Africa in 1944-45.

The examination of the live material sent by F. X. Williams was made possible by funds provided by the United States Navy and particularly the Office of Naval Research, enabling the author to go for the purpose to the Museum of Comparative Zoölogy of Harvard University. The author wishes to express his most sincere gratitude to Harold J. Coolidge, Executive Secretary of the Pacific Science Board of the National Research Council, for securing this grant; to William J. Clench for generously turning over to the author, for a period of a month, the complete facilities of the Mollusk Department of the Museum of Comparative Zoölogy; to his Assistant Ruth D. Turner for aid and assistance in many ways during his stay in Cambridge; to Joseph C. Bequaert for giving freely of his time and help during the course of this study and for identifying the species examined;[1] and finally to Henry A. Pilsbry of the Academy of Natural Sciences of Philadelphia, John Armstrong of the American Museum of Natural History, Yoshio Kondo of the Bernice P. Bishop Museum, W. Harry Lange of the University of California, and Dan Langford of the United States Navy, for the kind loan of preserved material.

[1] The taxonomic study of *Achatina* and *Archachatina* published in the same volume of this Bulletin (pp. 3–207) was written for the express purpose of clarifying the nomenclature, characters and classification of the species and subspecies examined anatomically by A. R. Mead and their close relatives. It was not possible to make at the present time a similar study of the other genera of Achatinidae dissected by Mead. I am however also responsible for the specific names he uses: in most cases shells of the lots or specimens he examined are now preserved at the M.C.Z., where they are available to future students and where their exact status may eventually be determined. The generic name *Pseudotrochus* is used by Mead in the customary sense of Pilsbry's Manual. It was shown recently that this name cannot be applied properly to this African group of snails. It seems hardly the proper place and would only cause confusion if the necessary change in nomenclature were proposed in a purely anatomical study.

JOSEPH C. BEQUAERT

GENITAL ANATOMY

The basic achatinid genital anatomy is of the most simple, generalized type — the only specialization of any importance being the penial sheath. There is a complete lack of any accessory structures along either the male or female conduit.

There are described below the genitalia of twenty-eight achatinid species and subspecies which the author has examined. The reproductive system of the familial type, *Achatina achatina* L., Figs. 1, 2, will be examined first from base to apex and in detail to establish the terminology that will be used hereinafter. This being understood, the genital structures of the other achatinids can be correctly identified, interpreted and homologized.

The figures of this species, as of the others, have been shown devoid of most individual variations and insignificant details, such as wrinkles, folds, and the like, which, if included, would needlessly obscure the valid characters and make more difficult the drawing of homologies. Further, the genitalia have been shown in the ventral aspect as they can thus be seen to better advantage.

Achatina (Achatina) achatina (Linné)

Figs. 1, 2

In this species, the penis (P) is a very muscular, robust, hollow tube that projects approximately half its length above the basally placed, thick penial sheath (PS) or "ring muscle." At the junction of the penis and the slender basal vas deferens (BD) the penial retractor (PR) takes its origin. This passes posteriorly to insert on the right tentacular retractor (TR) which is a portion of the great columellar muscle system. The basal vas deferens is embraced by the penial sheath for a portion of its length and hence comes to rest between it and the penis. It leaves the sheath, however, about midway and descends to the crotch between the penis and vagina. H. B. Baker (1939, etc.) refers to this crotch in related mollusks as the "penioviductal angle", though peniovaginal angle would seem more correct even if it is less euphonic. The basal vagina (BV), which is approximately as large and as long as the penis, is a very muscular, whitish, hollow tube without modification. Apically it is joined, after a slight constriction, by a more glandular, tan-cream colored portion of the vagina (AV). These histological differences, which are scarcely apparent in the preserved specimen, indicate that the two parts of the vaginal tube undoubtedly have different functions during copulation and egg laying. Nearly the entire vagina, but especially its basal portion, is held in

place on the ventral body wall by an irregular, variable series of muscle slips which, together, act during copulation as a retainer of the vagina. As these are taxonomically valueless it has been thought advisable not to confuse the outlines of the vagina by their inclusion. Basally the vagina combines with the penial tube to form a shallow genital atrium (GA), opening to the exterior through a single genital orifice. It is unfortunate that certain American and German authors have used the unsuitable terms "cloaca" and "Geschlechtskloake" for this common chamber in related species.

The spermatheca arises as a diverticulum at the very apex of the vagina. In this species, the spermathecal duct (SD) is extremely short and the terminal, clavate spermatheca proper (S) is only slightly longer. In the literature, this structure is variously referred to as a seminal receptacle, bursa copulatrix, spermatotheca and Samentasche, though spermatheca is by far the most generally used. Beyond the base of the spermathecal duct, the female conduit continues as the free oviduct (FO). This is only slightly larger and longer than the spermathecal duct.

The apical vas deferens passes in close juxtaposition to the vagina and is connected to it by thin slips of connective tissue. Apically, it joins the free oviduct to form the so-called spermoviduct (ovispermatoduct of Taylor, 1894, p. 146). Actually, this term is not wholly suitable as the entire oviduct, apical to the free oviduct, functions during egg formation as a uterus and only incidentally as an oviduct. As indicated below, the thin-walled, vitreous-yellow basal uterus (BU) probably forms the outer, yellow shell layer of the eggs, whereas the thick-walled, opaque-white apical uterus (AU) apparently forms the pale inner layers. The division between these two sections is pronounced.

At the point where the male and female conduits become confluent, the former develops a multifold, aciniform prostate gland (PA)which passes apically for the full length of the uterus and obscures from the outside the internally situated seminal duct, or spermatic duct. The interrelationships of these two conduits are discussed below under genital physiology. The female conduit is joined apically by a common duct from the reniform albumen gland (AG) and then fuses completely with the male conduit to form a very small, delicate tube. This common duct, which is sometimes referred to as the "carrefour" (H. B. Baker, 1939, etc.), soon gives off a short, irregular diverticulum termed the talon (T, Fig. 2). This indeed poorly understood structure consists of a basal sacculate portion and an apical digitiform diverticular process which in turn contains a varying number of smaller diverticula (*Cf.* Fig. 15). It has been variously, vaguely and erroneously

referred to in the literature of the achatinid genital system as "une poche ovarienne contenant les rudiments d'un œuf" (Deshayes, 1851), "vesicula seminalis" (Connolly, 1925), "spermatocyst" (Odhner, 1932), "Befruchtungstasche" (Simroth and Hoffmann 1908–28) and "caecum" (Reynell, 1906). Apical to the talon, the common duct becomes enlarged and extremely convoluted. The usual presence of a great mass of spermatozoa in this region of the duct vouches for the fact that it functions as a seminal vesicle (SV). In its apical portions, it may be found irregularly covered with a purple-black pigment. Somewhat beyond the middle, the ovotestis duct abruptly narrows to a very thin duct (OT) which passes to the ovotestis (O). This latter consists of five more or less distinct pinnate groups of acini embedded in the columellar surface of the antipenultimate whorl of the liver or hepatopancreas (L). In the freshly killed specimen, these are somewhat pinkish though they may be buried just deeply enough in the liver so that they are not apparent from the surface. And even in dissection, care must be taken in exposing them as they are very easily broken up and obscured in the all too soft liver substance.

Five specimens of *A. achatina* were examined. Three of these were collected by the author — one each from Accra, Gold Coast (June, 1944); Osenasi, Gold Coast (Oct., 1944), and Lagos, Nigeria (July, 1945). The female system in each of the latter two was markedly undeveloped though the male system was nearly as developed as that of the fully mature specimen from Accra. This undoubtedly is indicative of a protandrous condition in this species which also probably typically obtains in the other members of the family. The other two specimens were collected by Warren E. Buck in "Nigeria" some time in 1945 and were deposited in the California Academy of Sciences.

Measurements of Accra specimen in millimeters: P — 41, PS — 21x10, AV — 13, BV — 36, FO — 9, SD — 9, S — 10.

Achatina (Lissachatina) panthera (Férussac)

Fig. 21

Semper, 1874, p. 143, taf. xii, fig. 17.
Brancsik, 1893, p. 116, tab. vi, fig. 2.
Martens and Wiegmann, 1898, pp. 85–92, tab. iv, figs. 5, 6.
Pilsbry, 1904–05, p. xii, pl. 63, figs. 30, 32.
Simroth and Hoffmann, 1908–28, p. 564, pl. xxxv, figs. 9, 10.

Semper first described the genitalia of this species but he unfortunately had it confused with *Achatina fulica*. His specimens were reportedly from Calcutta which probably persuaded him to believe

that he had *fulica* — the sole species of *Achatina* in India. Another specimen (also undoubtedly *panthera*), which he states came from Zanzibar, was compared with these at the time and it was found that they "stimmte . . . in allen Einzelheiten überein." Since *panthera* has not been introduced into India, the validity of the locality of Semper's specimens (from "Dr. Anderson") is immediately open to question. Further, his illustration of the genital system clearly agrees with that of Brancsik[1] and those of Martens and Wiegmann and does not compare favorably with the existing illustrations of *fulica*. These three original illustrations all agree in the unique form of the penis. Pilsbry, and Simroth and Hoffmann copied the illustrations of Martens and Wiegmann.

A single large alcoholic specimen of the genitalia only of *A. panthera* was found in the collection at MCZ (58799). The information on the label leads one to believe that the specimen was collected on the island of Zanzibar by C. Cooke and given to F. C. Gray, and that he in turn gave it to MCZ on 26 March, 1862. Bequaert (1950), however, is convinced that *panthera* does not occur on Zanzibar and that "consul" Cooke probably obtained this specimen from some other East African place and shipped it from Zanzibar. Checking the shell under this accession number removed all doubt as to its being typical *panthera*. Furthermore, the form of the penis is indisputably like those of the illustrations mentioned above. It is extremely attenuate and, before connecting with the basal vas deferens, it folds back upon itself, well beyond the confines of the upper limits of its sheath, to form a conspicuous loop. Although the exposed basal vas deferens is, in diameter, only about half the size of the apical penis, this difference is superficially obscured by the broad origin of the penial retractor. This probably explains why these two adjacent parts have been shown in previous illustrations to be of the same caliber. The very slender sheath, which basally covers nearly three-quarters of the penis, is apically thin-walled and constricted by discernible circular muscle bands. In the absence of live material, the function of this constriction cannot be determined but it quite possibly is responsible for producing, during copulation, an unusual intromittent organ.

The sheath does not cover the most basal part of the penis, adjacent to the genital atrium, and there is thus formed what hereinafter will be referred to as a penial prepuce (PC). Its anatomical significance is treated below in the discussions of the penial types and copulatory anatomy. Basally, within the sheath, the penis becomes approximately twice the size of its most apical portion. A very short penial retractor

[1] Brancsik illustrates it under the new specific name, *mossambica*; this Pilsbry put in the synonymy of *panthera*.

inserts upon the tentacular retractor muscle. The vas deferens does not reach the peniovaginal angle. Just before its junction with the free oviduct, there is a fairly conspicuous, apparently lobulated and glandular mass whose possible function is explained below in the section on genital physiology.

The most striking element in the genitalia is the unusually attenuate vagina which basally is very muscular, thick-walled and thrown into a tight series of compound folds. The nature of the folds and the arrangement of the muscle bands seem to preclude any possibility of distortion, due to killing, being a factor in producing these folds. Previous illustrations of the genitalia of this species have shown what appeared to be very wrinkled vaginae; it is now quite apparent that these "wrinkles" were merely attempts to indicate the characteristic folds. Further, all specimens of the subspecies *lamarckiana* possessed similar but less pronounced folds. Upon dissection of the vagina, the lumen was found to be small and convoluted in conformity with the thick vaginal folds. Apically, the vagina is straight and thinner walled. The short free oviduct and the basal portion of the equally short spermathecal duct are of the same caliber as the apical vagina. The large, sacculate spermatheca is approximately twice the length of its slender duct. A distinct talon is present and, like the other apical structures, is typical of the group. The genital atrium is shallow.

Measurements in millimeters of the genitalia: P (apical to PS) — 30; PS — 42; PR — 13; AD — 57; BD — 3.5; V — 60; FO — 10.5; SD — 11; S — 23x7; AG — 21; No. compound curves, vagina — 8.

Achatina (Lissachatina) panthera lamarckiana Pfeiffer

Seven of sixteen alcoholic specimens of this subspecies (MCZ 4880) were examined. These were collected by Nicholas Pike in Mauritius on October 13, 1873. The seven were selected to give the greatest possible variation in body size.

No really tangible differences could be found between *lamarckiana* and typical *panthera* which could not reasonably be attributed to differences in size of the animal or artifacts of preservation. One significant fact was apparent, however; for though all specimens were sexually mature, none attained near the over all genital proportions of the single specimen of typical *panthera*. And to add significance to this, the two specimens of the closely related *A. layardi* were considerably larger animals than any in this series of *lamarckiana* and yet they both were quite immature. These findings, then, lend strong support to the assumption that *lamarckiana* is merely a small race of *panthera*.

Of particular importance, in the comparison of the seven specimens in this lot, is the great variability in the size of the penial "loop" that passes out of the sheath. It should be noted in the accompanying tabulation, however, that the length of the "loop" and the sheath are in inverse proportion, thus probably indicating a variable degree of contractility in these two organs. Of similar importance is the variable number of compound curves in the vaginae. Only one of the specimens possesses for certain, the circular muscle bands of the apical sheath found in the single specimen of typical *panthera*. Actually, a series of freshly killed specimens is needed to throw further light on these apparent differences. In all specimens, the penial retractor inserts upon the right tentacular retractor and the vas deferens does not reach the peniovaginal angle.

Measurements in millimeters of the genitalia:

P (apical to PS)	32	32	34	39	1	32	4
PS	19	15	22	21	32	26	34
PR	6	3.5	8	5	10	10	6
AD	29	24	37	30	26	33	28
BD (apical to PS)	3	5	2	4	—	8	1
V	22	23	27	24	25	31	24
FO	8	4	11	10	9	11	5
SD	10	6.5	13	8	11	11	6
S	10x4	10x3	13x6	11x4	18x8	15x5	13x5
AG	9	10	18	—	—	14	9
No. comp'd curves in vagina	2	6	4	5	3	7	3

Achatina (Lissachatina) layardi Pfeiffer

Two alcoholic specimens (MCZ 82409), collected by J. H. Sandground at Lourenço Marques, Portuguese East Africa, were dissected. One was so immature as to be practically valueless. The other, though somewhat immature, gave a quite fair idea of the definitive genital anatomy of this species. Basically, the genitalia are strikingly like those of *A. panthera* in that both the penial sheath and the vagina are attenuate and that the penis forms a long apical loop. The only tangible differences are found in the vagina which is not as muscular nor does it show even the slightest suggestion of forming the compound curves so characteristic of *panthera*. To add significance to this, the smallest individuals of the series of *A. panthera lamarckiana* examined, were smaller than this specimen of *layardi* and yet they possessed very muscular, sinuous vaginae. This suggests then that these vaginal characters may prove, upon examination of full-grown specimens of *layardi*, to be the only fundamental differences that exist between these two obviously very closely related species.

Measurements in millimeters of the larger specimen: P (apical to PS) — 27, PS — 13, PR — 6.5, AD — 27, BD (apical to PS) — 3, V — 17, FO — 7, SD — 10, S — 10x2.5, AG — 6x2.

Achatina (Lissachatina) glutinosa Pfeiffer

Fig. 20

There was but a single, fully mature specimen available for dissection. Its sole datum consisted of an American Museum of Natural History catalogue number "3221".

In many respects, the genitalia are intermediate between those of *A. reticulata* and *panthera*. As is shown in the conclusions, they thus form the last link in a series that nicely connects such anatomically diverse forms in this genus as *fulica* and *panthera*. The penis sheath is long and tubular. Apically, the penis is fairly large and projects for almost half its length beyond the sheath. Because in this specimen the adjacent basal vas deferens, which is less than half the caliber of the penis, is considerably shorter, it effects a sigmoid flexure in the penis thus producing a peculiar penial "loop." The very short penial prepuce is scarcely discernible. The vas deferens leaves the sheath in approximately its apical one-third and does not reach the penio-vaginal angle but passes directly to an apical swollen portion adjacent to the prostatic gland. An insertion on the right tentacular retractor is made by the fairly long penial retractor.

A very definite swelling is present in the basal vagina but it does not approach the rotundity or the cormoid proportions of those in *fulica* and closely related species discussed below. The apical vagina is slender in its mid-portions but nearly twice as large at the junction of the free oviduct and spermathecal duct. The latter is quite attenuate and terminates in a capitate spermatheca. The larger free oviduct narrows only slightly in its apical portions.

Of the species examined, *glutinosa* seems to be nearest to *reticulata* and differs only in that the basal vagina is more muscular, the apical vagina, the penis, and the sheath are longer and more slender. On the other hand, it can be distinguished from *panthera* in that the basal vas deferens forms a greater part of the "loop", the penial retractor is longer, the sheath is shorter, the shorter vagina is not sinuous, and both spermathecal duct and free oviduct are considerably longer. These differences notwithstanding, there is little doubt that *glutinosa* and *panthera* are definitely closely related.

Measurements of the genitalia in millimeters: P (apical to PS) — 15; PS — 20; PC — 3.5; PR — 28; BD (apical to PS) — 11; AD — 55x1.25; BV — 6x5; AV — 29x2-3.5; SD — 31x1.5; S — 9; FO — 28x2.25; AG — 28x11.

Achatina (Lissachatina) albopicta E. A. Smith

Figs. 14, 15, 16, 18

The very robust, thick-walled, white penis sheath, which is approximately half as wide as it is long, stands out as the most striking feature of the genitalia of this species. In direct contrast, the penis was found, upon opening this sheath (Fig. 16) to be extremely slender, thin walled and scarcely as large around as the basal vas deferens. The process of extroversion of these structures to form the intromittent organ seemed enigmatic until copulation was observed in *Achatina fulica* (*vide infra*). No demarkation between the penis and basal vas deferens could be found; though, as in other species, the origin of the penial retractor indicates the region of this junction. The penial retractor in its basal one-seventh is embraced by the sheath; apically it inserts on the right tentacular retractor. At the basal limits of the sheath, the internally contained penis is enlarged and then suddenly constricted at its junction with the unensheathed, thin-walled penial prepuce. This latter, like the adjoining genital atrium is lined with a brownish, chrome yellow epithelium. The epithelium gives rise to thick, chrome yellow slime as do the rich-brown colored exposed portions of the body. The basal vas deferens leaves the sheath about midway and extends approximately two and one-half times the length of the sheath to its junction with the free oviduct to form the sperm-oviduct.

A dissection of the basal vagina (Fig. 18) revealed that a very thick muscular band is responsible for the cormoid proportions of this organ. The apical vagina is thin-walled and nearly three times the length of its basal portion. The slender free oviduct and spermathecal duct are only slightly longer than the apical vagina. These three structures are approximately the same caliber as the apical vas deferens. The spermatheca is variable in length but remains relatively slender and clavate.

The basal uterus is a pronounced military green-brown in the freshly killed specimen and has numerous longitudinal vermiculations indicating good accommodation for a sizeable batch of eggs. The apical uterus is pale yellowish basally and pale cream color apically with the usual abundant transverse folds. The talon (Fig. 15) has a variable number of diverticulations. The convoluted seminal vesicle is basally pale cream colored and apically dark purplish.

There were dissected four live specimens collected in May, 1948, by F. X. Williams at Diani Beach, south of Mombasa, Kenya. The single immature individual which was examined was quite apparently protandrous.

Measurements in millimeters of genitalia (the illustrated specimen is listed first):

P	10	—	—	—
PS	14.5x7	16x7	15x9	16.5x8
PR (apical to PS)	22	19	22.5	20.5
PC	2.5	5	5	6
VD	39	40	38	41
BV	5x8	4x5	6x10.5	4x9
AV	13	13.5	15	15
FO	15.5	16	19	22
SD	19	18	16	23
S	11	8	17	17
AG	16.5	11	29x9	30x9

Achatina (Lissachatina) reticulata Pfeiffer

Fig. 13

In spite of the great similarity in the form and sculpturing of the shells of this species and *albopicta*, the genitalia are quite contrasting. The penis, like those of *A. achatina* and some species of *Archachatina*, is very large and muscular and extends considerably beyond the upper limits of the fairly thin-walled sheath. There is a marked difference in the caliber of the apical penis and the basal vas deferens. From their junction, the penial retractor passes to the right tentacular retractor where it makes the insertion. The first specimen dissected, which is the one illustrated here, has a highly significant modification of this insertion. A description and a discussion of this will be found below under the topic of penial insertion. The sheath is approximately only twice as long as the apically exposed penis and four times as long as the penial prepuce. The basal vas deferens leaves the sheath in its apical one-third and passes nearly to the peniovaginal angle before joining the free oviduct.

In this species, in contrast to *albopicta*, there is a conspicuous lack of a muscular thickening of the basal vaginal wall. The vagina is evenly thin-walled throughout its entire length and is not differentiated into basal and apical portions. It is somewhat enlarged adjacent to the shallow genital atrium and more strongly enlarged in its apical portions before giving rise to the slender spermathecal duct and the larger free oviduct. The spermatheca is variable but in general clavo-capitate. The basal uterus is canary-yellow and the apical uterus is pale cream in color; in other respects these structures are typical of the genus.

One juvenile and two adult live specimens, collected on the island of Zanzibar in June, 1948, by F. X. Williams, provided the material for the examination of the genitalia of this species. A fourth one was preserved but not dissected. The body is light tan in color with a washing of brown over the tentacles, head and neck. The largest one in the lot was seen twice to be rasping vigorously along the leading edge of its shell in an apparent robbing-Peter-to-pay-Paul attempt to add more calcium to its diet.

Measurements of genitalia in millimeters (in each case the first figure refers to the specimen illustrated): P (apical to PS) — 13, 8, 10; PS — 26, 12, 16; PR — 33, 13, 20; PC — 6, 2, 3.5; VD — 71, 32, 49; V — 39, 19, 20; FO — 29, 16, 23.5; SD — 32, 20, 26; S — 25x9, 9, 14.5; AG — 34x11, 9, 29x7.

Achatina (Lissachatina) iredalei Preston

Figs. 17, 19

Though this is a considerably smaller animal and its shell is of quite different form, the genitalia are infinitely more similar to those of *A. albopicta* than the latter are to those of the presumed more closely related *A. reticulata*. The penis sheath of this species, however, is much less incrassate than that of *albopicta*. The penis, which is typically completely contained within the sheath, is somewhat enlarged at its junction with the basal vas deferens. In only one case was this region seen to be projecting very slightly beyond the apical limits of the sheath. This apparent exception can be accounted for through the fact that, during the killing process, a greater contraction of the penial retractor tends to attenuate the ensheathed penis. The penial retractor takes its origin very broadly on the apical penis, the basal vas deferens and even the inner surface of the sheath. In every case, except one, the retractor inserts on the right tentacular retractor. The significance of this and other exceptions is discussed below. The sharp demarkation between the penis and the penial prepuce that was found in *albopicta* was also found in this species. The basal vas deferens leaves the sheath in its apical one-third and extends, as the apical vas deferens, approximately three and one-half times the length of the sheath.

The basal vagina is very muscular, enlarged and cormoid though not to the extent of that of *albopicta*. The most characteristic feature is the very abbreviated apical vagina which is approximately the length of the basal vagina. The free oviduct is slightly larger and the spermathecal duct is somewhat smaller than the apical vas deferens.

In general, these two structures closely resemble those of *albopicta*. The spermatheca is small and clavo-capitate. The basal uterus is bright butter-yellow in color. Other apical genital structures seem typical of the achatinas in general.

Five of the six live specimens, collected by F. X. Williams, were dissected. Two of these (Nos. 3, 20), including the one illustrated, were collected in May, 1948, at Diani Beach, south of Mombasa, Kenya; the other four (Nos. 12, 16, 21, 22) were collected in June, 1948, on the island of Zanzibar. One of these latter possessed a well-developed male system and a very immature female system indicating that protandry obtains in this species. No tangible differences whatsoever could be found in the anatomy of the specimens from these two localities. One specimen was found to contain five large albumen masses in the apical uterus; the significance of these is discussed below in the section on physiology.

Measurements of genitalia in millimeters (the illustrated specimen is listed first):

	#3	#12	#16	#20	#21
P	11	—	11	—	—
PS	11x4	10	11	10	13
PR	16	13	13	10	15
PC	2.5	2	2.5	3	2.5
VD	41	30	37	35	46
BV	5x5	2x4	3x5	2x4	3x4
AV	4	5	4	5	5
FO	13	11	17.5	13.5	18
SD	17	13	18	17	19
S	6.5	2.5	—	10	7
AG	38x7	4	24x7	27x7	23x9

Achatina (Lissachatina) zanzibarica Bourguignat

Figs. 8, 10

There were dissected, in the study of the genitalia of this species, six of several specimens collected by A. Loveridge in Amani, Usambara Mountains, Tanganyika Territory, in November, 1926. Unfortunately, the killing medium, in which these specimens were placed, was so severe that in most cases extreme distortion was found to have taken place in the soft parts of the snail. One in this lot, however, seemed to be in better condition than the rest; the genitalia of this specimen have been illustrated.

The proportions of the genital structures are so nearly like those of *A. iredalei* and especially *A. loveridgei* that they can be distinguished

only with difficulty. The penis is so abbreviated that the fairly thick-walled sheath not only covers it completely, but also embraces the penial retractor for approximately half its length. The penis seems to be divided almost equally into three quite definite regions. The most apical portion is only slightly larger around than the basal vas deferens, and in its connection with this latter, it forms an oblique angle. Only the very shortest part of the basal vas deferens is embraced by the sheath. This is in contrast with the condition in *iredalei*. The mid-penial portion is a very narrow, thin-walled tube, only one-half the caliber of the apical portion. This becomes much broader, but not abruptly so, to form the shorter basal portion. The latter appears to join the penial prepuce broadly but upon closer examination, a very narrow constriction is found between the two structures. The penial retractor, apical to the sheath, is narrow and shorter than the sheath. In two specimens it inserts upon the right tentacular retractor, in three specimens it inserts in the approximate center of the diaphragm and in one specimen it splits terminally and attaches at both places. The significance of these variations in insertion is discussed under that general topic below.

The cornoid, muscular basal vagina is sessile upon the genital atrium. The slender, thin-walled apical vagina is twice the length, but only slightly longer than the width, of the basal vagina. The free oviduct and the spermathecal duct are of the same caliber. They are approximately half the length and almost as wide as the vas deferens. The clavate spermatheca is about half the length of its duct.

Two of the six specimens were gravid with fully formed embryos. One contained twenty-six. Some of these had apparently been quickly expelled during the killing process, for six were found discharged in the folds of the foot and mantle, one in the genital atrium, and two in the free oviduct. The rest were found in the greatly distended uterus going apically to a point adjacent to the albumen gland. This latter was very small indicating that its supply of albumen had been heavily drawn upon. The other gravid specimen had been dissected previously by other investigators (Clench and Archer, 1930). There was no way of determining the number of embryos that this one contained though a single one was found centrally located in the free oviduct. The embryos varied from 3½ to 4½ whorls and from 11x9 mm. to 14.5x11 mm. in height. This phenomenon of ovoviviparity is treated below in a discussion of genital physiology.

Due to excessive distortion in two of the specimens, the measurements, in millimeters, of only four are given here. The specimen illustrated is listed first.

P	7	—	—	—
PS	11x5	19.5	14	19
PR	7	8.5	10	6
PC	3.5	3	11	2.5
VD	40	40	56	46
BV	3x5	3x4.5	—	3x5
AV	5	6	5.5	6.5
FO	19	22	—	16
SD	20	12	26	22
S	11	22	9	11

Achatina (Lissachatina) fulica fulica Bowdich

Fig. 41

Quoy and Gaimard, 1832–34, **2**, pp. 152–155; **3**, pp. 879–880, pl. 49, fig. 21.
Keferstein, 1862–66, pl. 99.
Brancsik, 1893, p. 204, tab. vi, fig. 6.

With an illustration of the internal anatomy of *Achatina mauritiana* (= *fulica*), Quoy and Gaimard were probably the first to show the achatine genitalia. The lack of detail, however, makes it of little value, especially since much of their terminology is now known to be incorrect. Keferstein copied their illustration directly. Semper (1873) unfortunately used the name *fulica* in describing and illustrating *A. panthera* (*q.v.*) thus later persuading Pilsbry (1904–05, p. xii) to assume that the genitalia of these two species were similar. Brancsik illustrated, rather poorly, the genitalia of a *fulica* from Madagascar, therefore of the typical subspecies. The proportions of the basal female conduit are approximately correct; but the lack of detail in the male system makes the illustration practically valueless. Further, he erroneously interprets the penial retractor as the "flagellum."

In the present study of the genitalia of this species, there were dissected and examined: two specimens collected in Mauritius by Nicholas Pike in 1873; one specimen collected at Agaña Bay, Guam, by R. Tucker Abbott; two specimens raised in Hawaii in 1940–41 by Yoshio Kondo; three of several specimens collected on Saipan (one on November 11, 1947, and two on March 12, 1948) by W. Harry Lange; and two of several immature specimens and a number of empty shells collected on the Palau Islands in the fall of 1948 by Dan Langford. Before any of the material was examined, seven freshly killed specimens of *A. fulica hamillei* from Kenya and Zanzibar and two freshly killed specimens of *A. fulica rodatzi* from Zanzibar were dissected and the relationships of the genitalia were determined and

illustrated (Figs. 5, 7, 11, 12). As there had not been found any appreciable difference in the genitalia of *hamillei* and *rodatzi*, it was not expected that those of *fulica fulica* would prove different. The results of these examinations were confirmatory. The figures indicated above, then, will serve to illustrate as well the genitalia of the typical subspecies. The same degree of variability in the length of the penis, apical vagina, free oviduct and spermathecal duct was found in this series of typical *fulica*. In a smaller series, however, these differences might have been judged as significant. In every case, the penial retractor inserted on the right tentacular retractor. A generalized diagram (Fig. 41) based on the genitalia of all examined specimens of *fulica* subspp. has been prepared to demonstrate relationships and facilitate homology in the various penial types, which aspects are treated in detail below.

The specimens from Saipan and the Palau Islands show definite signs of being in an environment that is far from optimum for them. In the first place, nearly all of the shells showed the results of multiple, clean, sharp breaks with often as much as an inch or two of the last whorl of the shell being removed. In a couple of instances, new shell had been built up and this too had become broken. Breaks higher up on the shell had also been mended, leaving noticeable irregularities in the outline of the shell. To add to this effect, much of the tissue of the snail contained numerous whitish islets of calcification, giving a measly quality to the flesh. All this presented a superficial picture of a very unthrifty condition in the snails. And, as a matter of fact, these were sent to the author with the suggestion that possibly they were diseased snails.

In the absence of first-hand knowledge regarding the environmental conditions in the region where these specimens were collected, it is a bit difficult to state what caused these breaks. But a very likely guess can be produced. These giant snails have a rather bad habit of taking a short cut to the ground after foraging in the tree tops. In the West African rain forests, the author has observed *Archachatina degneri* dropping from the tree tops with impunity because of the dense undergrowth. However, in the region where the specimens of the former species were collected, the undergrowth quite likely was insufficient to break their fall. Beyond this, rough, coralline rock may have been in the way. This could have produced the sharp breaks evident in the shells. If a predatory vertebrate had produced the breaks, in the process of eating the snails, specimens would not be commonly found that had the snail still intact.

Another factor adds to this. There are definite periods of rain and drought in that region. Snails with badly broken shells would be hard

put to withstand the unfavorable conditions of increased dryness since they would be unable to withdraw completely into their shells and form the protective epiphragm. Such snails would eventually become sufficiently dehydrated to die, or become subject to the attacks of predators or disease agents.

The calcification of the tissues comes very naturally from a diet high in $CaCO_3$. The specimens raised by Yoshio Kondo in Hawaii were fed a diet high in $CaCO_3$ (as evidenced by coralline flakes in the contents of the digestive tract) and the tissues of these were in the same condition. This has been observed in other mollusks on similar diets. Because of the unsightly nature of these pale beads of $CaCO_3$ all through the tissues, however, one might be persuaded to believe that an actual pathogenic condition was present.

Absolutely no other factor could be found nor was there even the slightest evidence of any pathogenesis. On the contrary, the tissues looked very healthy and normal. It will, of course, take field work to determine for certain whether or not an actual "disease" has gotten started in *Achatina fulica* in these regions. One thing is certain though, the specimens at hand indicate nothing more than breaks in the shells produced by a mechanical force of considerable strength and calcification of the tissues due to the normal process of storing excess $CaCO_3$ taken in a $CaCO_3$-rich diet.

The specimens in the lot collected on Saipan on November 11, 1947, were remarkable in that they were all very small, yet several of them were gravid. Somewhat over seventy eggs were found in the one specimen that was dissected. Though the genitalia were histologically mature, they were diminutive in size. This "dwarfism" is undoubtedly attributable to limited feeding imposed by the marked dry periods on that island. There are also strong indications, in the material from the Palau Islands and Saipan, that these periods of dryness effect at least a partial seasonal atrophy of the genital system inasmuch as in some cases the genital structures are markedly reduced in caliber though not immature. In some of these and in some of the functionally mature specimens, the apical portion of the penis forms a very definite loop, of one to three millimeters, apical to the apparently shortened or contracted sheath. It is quite obvious that field work in these regions is needed to determine for certain the significance of these variations.

Actually, it was the study of the genitalia alone that provided the first tangible evidence of the true conspecific nature of these three subspecies. Further, this study has at last permitted us to connect indisputably the "*fulica*" that has spread from Mauritius to India to the Dutch East Indies to China to Japan to the South Pacific

Islands to Hawaii and even to unsuccessful invasions of our own country, with the prototype stock (*fulica hamillei*) of continental East Africa. Such information is obviously of great importance in determining more effective control of this rapidly spreading agricultural pest as it indicates where a study can be made of this snail in its native environment.

With the genitalia of these three subspecies being essentially identical, Bequaert (1950) has distinguished them on the basis of minor differences in the shells.

Measurements of genitalia in millimeters:

	Mauritius		Guam	Hawaii		Saipan		
P	13	—	—	12	15	9	16	8[1]
PS	14	15	12.5	14	14	6	15	7
PC	5	5	3	6	3	3	2	4
PR	15	9	40	20	32	37	33	—
VD	51	40	49	48	57	43	46	27
BV	4x5	3.5x4.5	4x5	3.5x5	4x5	2x2	3x4	3.5x3
AV	10	10	13	10	12	7	8.5	5
SD	20	14	31	21	34	32	30	11
S	10	10	12	14	13	7	9	5
FO	22	12	31	21	37	33	29	8
AG	—	—	—	62x14	—	5	15x4	13x7

[1] Gravid.

Achatina (Lissachatina) fulica hamillei Petit

Figs. 5, 7, 11, 12

Pilsbry, 1904–05, pp. xiii, 45, 216, pl. 65, figs. 65, 66.
Bacci, 1939, p. 335, fig. 1.

As shown below, Pilsbry first described the genitalia of this subspecies (as *A. leucostyla*), from Wasin Id. near Mombasa. Bacci dissected specimens from Italian Somaliland, which he called "*Achatina fulica* (Fér.)." His illustration was mediocre. His description of a peculiar "piccolo diverticolo cieco . . . con due piccole protuberanze sferoidali" probably refers to the talon though his illustration suggests that adjacent larger genital structures may have confused him.

Seven live specimens collected by F. X. Williams were examined. Four of these (Nos. 1, 6, 13, 18) were collected at Diani Beach, near Mombasa, Kenya in May, 1948. The other three (Nos. 7, 11, 19) were taken on Zanzibar in June, 1948.

The penis sheath is slender, but quite muscular, and often subarcuate. Thin muscle bands originating in the basal portion of the

sheath pass onto the thin-walled penial prepuce and may obscure the junction between these two structures. In every case the penial retractor inserted on the right tentacular retractor. The penis, like those of the closely related *Achatina albopicta, iredalei, zanzibarica* and *loveridgei*, is very slender and completely enclosed by the sheath. A great deal of variation was seen in the length of the penis. In some (Fig. 5) it is so short that it joins the basal vas deferens almost at right angles. In others (Fig. 11) there is formed a definite hairpin loop which very nearly projects beyond the confines of the sheath. There is no evidence that differences in the degree of contraction could make up more than a fraction of this difference. Besides, the shorter penes do not appear to be contracted any more than the longer ones. The basal portion of the penis is swollen and is about as thick-walled as the penial prepuce, between which two structures there is a noticeable constriction. Centrally, the penis is very slender and thin-walled; whereas in its apical portions it is large and clavate. In this latter region, the muscular wall is far thicker than any place along the vas deferens and hence an ejaculatory function can probably be assigned to it (*Cf.* Fig. 41). As will be seen below, a study of the copulatory anatomy tends to substantiate this assumption. Numerous fine muscle strands pass from the point of origin of the penial retractor, on the penis and adjacent vas deferens, to many points on the inner wall of the sheath. The vas deferens reaches the peniovaginal angle.

The basal vagina is thickly muscular and cormoid as it is in the four achatine species mentioned above. Apically the vagina is slender, thin-walled and proportionately longer than any of those except *albopicta*. There is a definite variability in the length of the spermatheca duct and the equally slender free oviduct which is approximately the caliber of the vas deferens. Similarly, the spermatheca may be clavo-capitate or so slender that it forms only the slightest terminal enlargement. There are shown in Figs. 7 and 12, from Kenya and Zanzibar respectively, these extreme variations, which also have been found occurring at random and without significance in populations of the typical subspecies. The apical genital structures are typical of the genus in form and color. Specimen No. 11 was observed in copulation with a specimen of *A. fulica rodatzi* and details of the observations are discussed below under that topic. Upon dissection, specimen No. 19 was found gravid with 292 lemon-yellow colored eggs which had heavy calcareous shells measuring 4x5 mm. The relationships of the eggs to the genital system are treated below in the discussion of that general topic.

Pilsbry described members of this subspecies as the new subspecies *leucostyla* of *Achatina panthera;* but in the same manuscript, he later

(p. 216) elevated the name to full specific standing, with this statement, "This form proves to be so different in genitalia from *A. panthera* that it will stand as a species." There was thus established for the first and only time in this group, until the present study was undertaken, a new species on the basis of genitalia.

The paratypic series of four specimens of Pilsbry's *leucostyla*, from Wasin Island, Kenya Colony, was loaned to the author by the Academy of Natural Sciences of Philadelphia to permit a comparison with the live material from Zanzibar and Diani Beach, Kenya. As suspected when the first specimen from this latter place was dissected, *leucostyla* and *hamillei* are conspecific. Their genitalia compare favorably in every detail. Since this confirmation was made upon the examination of the first paratypic specimen of *leucostyla*, the other three paratypes were left undissected for possible future anatomical examinations. The single specimen examined had been previously only partly dissected, presumably by H. A. Pilsbry, and the genitalia were still left intact save for the basal parts which had been freed at the genital orifice and lifted out a ways. When the penial retractor was fully exposed, it was found to be bifurcated at the tip with part inserting normally on the right tentacular retractor and the other part passing around the sagittal myoseptum in straddle fashion and inserting on the columellar muscle. As will be seen below in the general discussion of the insertion of the penial retractor, it was such specimens as this that finally solved the mystery of the occasional and overrated diaphragmatic insertion of this muscle.

Measurements of genitalia in millimeters (those marked with an asterisk have been illustrated in this paper):

	#1*	#6*	#7*	#11*	#13	#18	#19	*leucostyla*
P.....	14	11	12	—	10	12.5	11	14
PS.....	14	13	12	—	12	15	11	17
PC.....	5	5	6.5	—	4.5	5	3.5	3.5
PR.....	24	19	19	18	24	20	14.5	50
VD.....	67	56	48	56	51	57	55	58
BV.....	3.5	3.5x5.5	4x5	4x6	3x4.5	3x5	3x7.5	4x5
AV.....	9.5	8	11	11	8.5	7	14	16
SD.....	40	28	18	28	28	33	—	40
S.....	12	9	12x5	15x4	8	11	—	10
FO.....	35x1.5	26	18	28	27	27	20	35
AG.....	25	18	29	33x10	21x7	35x12	24x10	48x17

Achatina (Lissachatina) fulica rodatzi Dunker

Pilsbry, 1904–05, p. xiii, pl. 64, fig. 68.

The genitalia of this subspecies were illustrated by Pilsbry under the new name *Achatina chrysoleuca*. The completely enclosed penis was not shown, though he states that it is "similar to that of *leucostyla* but longer." It should be recalled that *leucostyla* has been shown above to be synonymous with *A. fulica hamillei* and that there is a natural marked variation in the length of the penis in both that subspecies and typical *fulica*. This would then suggest that there was little or no real difference between *hamillei* and *rodatzi*. Examination of other subspecies complexes has taught us so far that tangible subspecific differences in the soft anatomy do not exist. It was therefore assumed that the genitalia of *rodatzi* (= *chrysoleuca*) would be like those of the other two subspecies. An examination of the two live mature specimens of *rodatzi*, collected by F. X. Williams on Zanzibar in June, 1948, clearly indicated that this assumption was a correct one. Further, the "type" specimen of *chrysoleuca* (Acad. Nat. Sci. Phila. 68113, collected by Dr. A. Donaldson Smith in Tulu Didirko, E. Africa on March 27, 1895) was examined by the author and was found to be mature and essentially identical to the Zanzibar specimens. Once again, subspecific characters seem to rest exclusively in the shell characters. In this pale subspecies, the body is a yellow-tan color and the head is slightly brownish.

The second of these two specimens copulated with a specimen of *A. fulica hamillei* and the details of this process and their anatomical significance are discussed below under a separate heading.

Measurements of genitalia in millimeters (in each case, the number in parentheses refers to the type specimen of *chrysoleuca*): P — —, 11, (7); PS — 14, 14, (14); PC — 4, 4, (—); PR — 14, 15, (26); VD — 59, 57, (35); BV — 4x6, 3x5, (3x4); AV — 11.5, 9.5, (8); SD — 27, 20, (18); S — 9, 15, (12x5); FO — 27, 21, (16); AG — 38x15, 39x15, (26x10).

Achatina (Euaethiopina) loveridgei (Clench and Archer)

Figs. 6, 9

Two paratypic specimens collected in Bagilo, Uluguru Mts., Tanganyika Territory, were examined. These had been previously dissected by Clench and Archer (1930).

In only a few respects do the genitalia differ from those of *A. iredalei* and even less so from *A. zanzibarica*. The penis and the basal half of

the penial retractor are completely embraced by the sheath which is proportionately somewhat shorter than in *zanzibarica*. With respect to its sheath, however, it is proportionately larger in its apical third and smaller in its basal two-thirds. Apically, the penis joins the basal vas deferens at right angles. The very wide penial retractor originates broadly on the apical portion of the penis, the entire ensheathed portion of the basal vas deferens and adjacent portions of the inner sheath wall. No evidence of the manner of insertion remained in either specimen though Clench and Archer maintained that the retractor "inserted on the diaphragm." The vas deferens is somewhat shorter than in *zanzibarica* and leaves the sheath in its apical one-third.

The cormoid basal vagina is as long as, or almost as long as, the abbreviated, thin-walled, apical vagina. In this respect, it compares more favorably with *iredalei*. Basally, the free oviduct and the spermathecal duct are nearly the same caliber, though the latter is as slender as the vas deferens throughout most of its length. The former is approximately one-third the length and twice the diameter of the vas deferens. The spermatheca is capitate. No significant difference was found in the apical genital structures.

Clench and Archer (1930, p. 297) give the following characters to distinguish from *Limicolaria* the new genus *Euaethiops* (= subgenus *Euaethiopina* of *Achatina*) in which they had placed *loveridgei:* " . . . a larger, thicker albuminiparous gland; a shorter hermaphroditic duct, smoother above but heavily granulose at its entrance into the spermoviduct instead of consisting of a long series of granulations as in *Limicolaria;* a large uterus; a wider, fatter and shorter spermatheca; a longer, more twisted vas deferens; a larger penis; and a much shorter, thicker penial retractor." None of these characters is of generic grade. As a matter of fact, the first two can never be safely used even in distinguishing species. An examination of their dissections revealed the fact that only the outer layers of the thick penis sheath had been removed and the slender, tubular penis was therefore not seen by them at all. Hence the penis was reported and illustrated as being much larger than it actually is. As will be seen in a discussion of *Limicolariopsis kivuensis* (*vide infra*), this misinterpretation caused them to miscalculate in constructing the affinities of *Euaethiops*. Further, they incorrectly describe the ovotestis as "short, granulose and bound tightly to the albuminiparous gland." This gland is very disperse and located in the antipenultimate whorl of the liver as in other achatinas. It is the apical uterine folds that they apparently described. They made other observations which are at variance with the author's findings; but as they are less significant, space will not be taken here to comment upon them. Actually, there is little doubt that the general

form of the genitalia places *loveridgei* in the genus *Achatina* and close to the *zanzibarica-iredalei-fulica-albopicta* complex.

Measurements of genitalia in millimeters (the first figures, in each case, refers to the specimen illustrated): P — 11, (--); PS — 10x3, (12); PR — 4, (5.5); VD — 31, (34); BV — 2.5x4, (3x4); AV — 4x2, (3); FO — 11, (12); SD — 15, (11); S — 8, (10); AG — 23x9, (22x5).

Archachatina (Archachatina) bicarinata (Bruguière)

Fig. 25

Deshayes, 1851, **2**, pp. 154–155, pls. 127A (colored), 127B (colored), 127A127B (one uncolored plate).
Pilsbry, 1904–05, p. xiv, pl. 63, fig. 29.

This remarkable, large, sinistral snail was first anatomically examined by Deshayes (1851). He referred to it, however, as *Achatina sinistrorsa* Chemnitz. Though he did not discuss the genitalia, his exquisite illustrations of the animal, in successive stages of dissection, and the extensive labeling (explained in the Atlas, **1**, p. 18) leave little to the imagination. It is understood, of course, that at that early date, some of the genital structures were not correctly interpreted. For example, he refers to the prostate gland as a "portion du testicule", the ovotestis duct as "l'ovaire", the talon as "une poche ovarienne contenant les rudiments d'un œuf" and the vagina as "le col de la matrice." Pilsbry reproduced the illustration showing the genitalia of this species and pointed out that the manner of insertion of the penial retractor is "unknown."

Very fortunately, three alcoholic specimens of this genotype were obtained on loan from the American Museum of Natural History to permit a rechecking of the genital anatomy. These carried the following data: "J. G. Comia, San Thomé Is. A.6280." It was only with the greatest difficulty that two were removed from their shells, and then only after prolonged soaking in 0.8% solution of trisodium phosphate. As two specimens were adequate for the present study, it was thought advisable to leave the third one for possible future investigations.

It must not be forgotten that not only the shell is sinistral, but the entire animal is just the reverse of one that is dextral. The genitalia are therefore shown in Fig. 25 quite differently arranged, though with the same orientation as the other illustrated genitalia.

The species has, without question, the most muscular and proportionately the largest of the achatinid genitalia examined. The relatively huge penis is a hollow, muscular structure that projects apically

beyond the sheath one and one-half times the length of the latter. In both specimens, the apex of the penis is bent back on itself. A possible explanation for this is found in the fact that the penis apex tightly abuts against a vertical sheet of tissue (the sagittal myoseptum) a small portion of which is shown at the insertion of the very short penial retractor on the *left* tentacular retractor. The significance of this sheet of tissue is discussed below under the heading, "Insertion of the Penial Retractor." When the sheath was longitudinally cut, it was found to increase in thickness basally. Conversely, the penis was found to be reduced to approximately one-quarter of its apical width; thus the entire structure appeared markedly clavate. At the very base in both specimens, the sheath becomes somewhat sacculate, but this may be only an artifact of preservation. The vas deferens is of small caliber. It leaves the sheath approximately midway and passes to the peniovaginal angle. Internally, the penis is lined with a most remarkable papillo-rugate reticulation that is reminiscent of the lining of a rumen. It must, indeed, make a formidable organ when everted as the papillate rugae are so arranged that they would still remain distinct on the extroverted and distended organ. These papillate rugae are less abundant basally though they do continue right into the almost non-existent genital atrium.

The vagina is shorter than the penis sheath and is without any noticeable differentiation. Apically, it is continuous with the free oviduct, of approximately the same caliber. At the junction of these two structures is the very narrow spermathecal duct which terminates in a capitate spermatheca.

With a penis of this caliber, a short vagina, and a very slender spermathecal duct, it is difficult indeed to understand how the genitalia function during copulation.

Measurements of genitalia in millimeters (the first figure, in each case, refers to the specimen illustrated): P (apical to PS) — 60x8–10, (47x9–12); PS — 41, (31); PR — 18x8, (21x8); BD — 58, (78); V — 31, (32); SD — 31, (27); S — 19x9, (32x2); FO — 21x8, (28x10); AG — 38x14, (—).

Archachatina (Calachatina) degneri Bequaert and Clench

Fig. 4

Unlike that of the preceding species, the penis sheath extends only about a third of the way up the penis and the slender vas deferens leaves it somewhat below the half-way mark. From there it passes to the peniovaginal angle. There is a strong tendency for the basal

vas deferens to be shorter than the penis and as a consequence, the penis is drawn partly or often almost completely back upon itself. The penial retractor is long and inserts, in all cases observed, on the right tentacular retractor.

The vagina is shorter than in the anatomically similar *A. achatina* and enlarges gradually in its apical portions. Internally, there is a strong circumferential thickening of the muscle layers in the female conduit at the junction of the free oviduct and the vagina which is apparent externally as a shallow crease. It is conceivable that this acts during copulation as a sphincter to insure the entry of the penis into the spermatheca rather than the free oviduct. In contrast to that of *A. achatina*, the spermathecal duct is very long and slender and only a quarter to a third the size of the very robust free oviduct. The capitate spermatheca is sharply set off from its duct. Further apically, the structures are typical of the genus and bear no specific difference.

As will be shown in the conclusions, the similarity between *A. achatina* and the dolichophallate species of *Archachatina*, because of convergent evolution, is more apparent than real.

Twelve specimens, all collected by the author in Accra, Gold Coast, or its immediate vicinity, were examined between June and November, 1944. Immature specimens indicated the presence of protandry. One of the half-grown specimens was kept in a container without food or water and in a few days responded by forming a very thick, calcareous epiphragm that was complete except for a thin slit over the pneumostome. It remained quiescent for nearly six months and actually did not break the epiphragm and crawl about until water was sprinkled over the specimen.

Average adult measurements in millimeters: P — 51, PS — 18, V — 25, FO — 14, SD — 16, S — 10.

Archachatina (Calachatina) marginata ovum (Pfeiffer)

Fig. 3

Semper, 1873, p. 144.

Semper examined but did not illustrate the genitalia of "*Achatina marginata*" and found them typical and similar to those of *Archachatina granulata*.

In this species, the penial sheath is twice as long as in *Arch. degneri* and therefore the penis-sheath linear ratio nearly exactly attained the proportions (2 : 1) of the same structures in *A. achatina* (Fig. 1). As in *Arch. degneri*, though, the real differences are found in the female conduit. The vagina is large, tubular and unmodified save for a

whitish, more muscular basal portion that often is set off from the more glandular apical portion by a slight constriction. The spermathecal duct is very slender and in strong contrast to the capitate spermatheca. The free oviduct is equally long and approximately three times as large around as the spermathecal duct.

In every case, the long penial retractor inserted on the right tentacular retractor. As in the two previous species, and in *A. achatina*, the sheath is situated so far basally that a penial prepuce is not apparent.

Eight specimens collected for the author in the market place at Lagos, Nigeria, (5 in March and 3 in June, 1945) were examined. All possessed the diagnostic rich apricot-yellow columella.

Average measurements in millimeters: P — 63, PS — 32, AV — 20, BV — 5, FO — 13, SD — 17, S — 9.

Archachatina (Calachatina) marginata suturalis (Philippi)

The genitalia of this subspecies are so nearly identical to those in *Arch. marginata ovum* that they could not be distinguished. The three functionally hermaphroditic specimens that were examined, were collected in Lagos, Nigeria, in June, 1945, along with the specimens of *ovum*. It is not probable that a larger series will disclose consistent differences in the genitalia. The columellae of all three specimens were vinaceous-red in color.

Archachatina (Tholachatina) simplex crawfordi (Morelet)

Figs. 27, 28, 29

Pilsbry, 1904–05, p. xiii, pl. 64, figs. 69–71.

Two fully mature specimens, bearing the data: "Port Elizabeth, So. Africa, John Ponsonby 1889. Acad. Nat. Sci. Phila. 60967", were examined. One of these had been dissected and illustrated by Pilsbry as "*Cochlitoma crawfordi*." In this specimen, Pilsbry found the penial retractor attached to the floor of the diaphragm; this was confirmed by re-examination. The second specimen was still in its (broken) shell. This was removed and dissected. The short penial retractor was found to attach, as in most other achatinines, to the right tentacular retractor! Had Pilsbry dissected this along with the other specimen, he would have found that he could not safely give taxonomic significance to diaphragmatic insertions of the penial retractor. Actually, the penial retractor inserts at the junction of the right tentacular retractor and a vertical sheet of tissue, the sagittal myoseptum (discussed below). A portion of this latter is shown attached (SM) in Fig. 27.

When the thin-walled penial sheath was cut, a truly unique clavo-capitate penis was exposed. It was found to be broadly convex on one side and deeply concave on the opposite side, thus appearing thickly "U"-shaped in cross section (Fig. 29). The basal vas deferens attaches to the dorsal fold of this "U". It is this concave or infolded portion that Pilsbry considered a continuation of the vas deferens into an internal "fleshy pilaster." An examination of this latter, however, shows it to be of the same thickness and histological construction as the convex portion. It would undoubtedly form an asymmetrical swelling on the distended intromittent organ but it would not act as a pilaster *per se* as such would presumably be a stimulatory, solid ridge. The basal portion of the penis is thicker walled. The vas deferens reaches the peniovaginal angle and is embraced in that region by the penial sheath. In this specimen, the vagina is short and appears to be excessively wide because of pressure from adjacent structures. Both the free oviduct and the capitate spermatheca and its duct are longer than the penis.

The specimen that Pilsbry examined is almost identical in every respect with the exception of the vagina which is longer and more slender and in these respects is probably more typical. In Pilsbry's illustration, the spermathecal duct seems disproportionately long.

Measurements of genitalia in millimeters (the first figure, in each case, refers to the specimen illustrated): P — 6.5x2.75, (5); PS — 7x3, (—); PR — 2.25, (2); VD — 19, (20); V — 4.5x4, (5.5x2); SD — 11, (12); S — 5x2.5, (4x1.5); FO — 9, (12); AG — 8, (9).

Archachatina (Tholachatina) meadi Bequaert

Fig. 22

A single completely dehydrated specimen (MCZ 81351), collected in Ngosi Volcano, Rungwe, Tanganyika Territory by A. Loveridge on April 17, 1930, was soaked forty-eight hours in an 0.8% solution of trisodium phosphate. At the end of this time, the tissues were very pliable and, with the exception of the large, thin-walled spermatheca and its duct, the genitalia were removed without damage.

This specimen had been labeled "*Euacthiops loveridgei*." An examination of the genitalia, however, immediately indicated that a quite different animal was at hand. A comparison of the shell under this accession number with the types of *loveridgei* proved confirmatory. The penis is large, muscular and in every respect typical of the genus *Archachatina*. No internal papilla or verge is formed, though the apical third of the penis projects well out of the fairly thin, basally

located sheath. A very abbreviated penial prepuce is scarcely discernible. The basal vas deferens joins the apical penis to form a conspicuous loop apical to the sheath. The vas deferens is approximately one-half the diameter of the penis, leaves the sheath in its apical third, does not appear to reach the peniovaginal angle and describes a quite direct route to the spermoviduct. The very narrow, long retractor takes a broad origin on the penial loop and passes by a devious route, described in greater detail below in the discussion of this general topic, to an insertion centrally on the diaphragm.

The vagina is thin-walled, quite evenly tubular throughout its length and without any basal muscular swelling. Only the frayed basal part of the spermathecal duct was recovered; its proportions are therefore unknown. The cylindrical free oviduct is slightly smaller and shorter than the vagina. Nothing of significance was found in the apical genital structures.

Measurements of genitalia in millimeters: P (apical to PS) — 2.5, PS — 5x3, PR — 23, VD — 15, V — 9x2, FO — 8, SD — ?, S — ?, AG — 8x5.

Archachatina (Tholachatina) osborni afromontana (Bequaert and Clench)

Figs. 23, 24

There were examined in the anatomical study of this species, five preserved specimens collected for the Institute of the Belgian Congo National Parcs, bearing the data "Kamatembe (North of L. Kivu, Belgian Congo) 1059, G. F. de Witte."

In direct contrast to *bicarinata*, the genitalia of this species are proportionately so small that they probably represent the ultimate or near-ultimate in reduction in this genus, and perhaps even in the Achatininae. The penis, though diminutive, is not the delicate structure that is found in the *fulica* complex. It is fairly thick-walled, quite wide, without verge formation and entirely enclosed within the sheath. A definitely shaggy appearance is given to this latter because its surface is covered with many thin, narrow muscle bands which originate more or less centrally, become more abundant basally, and insert on or adjacent to the atrial wall. In two of the five specimens, the short penial retractor inserts medially on the diaphragm near its junction with the anterior lip of the mantle and the body wall. In the other three, it inserts on the body wall, in the neck region, anterior to this junction. The combination of a short penis and a short retractor has quite probably predisposed the retractor to this unusual insertion.

From the broad origin of the retractor on the penis and adjacent basal vas deferens, numerous muscle bands, similar to those on the outer surface of the sheath, interlace and pass to the inner wall of the sheath. These are made more apparent by similarly inserting muscle bands that have their origin in the outer muscle layer of the penis. This multiplicity of muscle bands produces a general untidy effect. Apical to the sheath, the basal vas deferens doubles in size with increased musculature. Further apically, it is somewhat reduced in size but becomes typically enlarged at its junction with the spermoviduct. This latter enlargement was cut open. Its walls did not seem excessively glandular and internally there were numerous, longitudinal trabeculate ridges.

The completely unmodified vagina is even shorter than the penis and almost as wide. The very large, sacculate spermatheca is disposed so far basally that early in the dissecting it might easily be mistaken for the penis. The free oviduct is proportionately long.

Only one specimen was immature. In this, the penis projected for half of its length beyond the short sheath thus creating a condition that superficially seemed in strong contrast to that in mature specimens. The rest of the structures, though reduced in size, were fairly typical — including the enlarged spermatheca.

Measurements of genitalia in millimeters (the first listed is illustrated in Fig. 23, the third is illustrated in Fig. 24):

P	7.5	—	—	—
PS	9.5	7	7x4.5	8
PR	15	—	8	12
VD	41	32	32	34
V	6.5	4	5x3	6.5
SD	4	4	4	4
S	22x8	21x8	15x6	12x7
FO	21	25	21x2.5	24
AG	19x4	22x4	11x4	20x5

Limicolaria kambeul (Bruguière)

Figs. 26, 30

Lehmann, 1864, p. 48, pl. 1, fig. 3.

In this species the penis sheath is apically so situated that it actually embraces the basal portion of the relatively short penial retractor, which latter inserts upon the right tentacular retractor. Since the sheath muscular elements pass imperceptibly onto the basal vas

deferens, there is no detectable division between the two structures. Basally, the sheath is delimited approximately half-way down the penis, though very thin muscle strands are seen to pass further down and blend with the otherwise naked muscle wall of the basal penis. Though the vas deferens, which does not reach the peniovaginal angle, is apically a fairly large duct, it is found basally to be about half that diameter. The vagina is only slightly larger at its apex than at its base and appears to be more or less evenly muscular throughout. The free oviduct, which attains a greater length than the penis, has only half the diameter of the very short spermathecal duct. The spermatheca is a broadly spatulate structure which attenuates apically and then enlarges somewhat to form a terminal bulbous portion. The genital atrium is pronounced. The basal and apical portions of the uterus are distinct. The prostatic acini are proportionately large and fewer than in any of the preceding species.

The thin-walled sheath was cut to expose the internally contained penis. The musculature of the penial retractor, the penis proper and the penial sheath is so extensive that it appears to be but a single tissue entity. A dissection of the penis itself, however, revealed relationships quite unlike anything found heretofore (Fig. 26). In approximately the middle of the penial organ is a pronounced circumferential thickening of the inner wall so that the lumen in this region is reduced to a very narrow passage. As this conical thickening projects into the basal half of the penial tube, it assumes the form, and undoubtedly the function, of a verge (penis papilla). Apical to the verge, the penial wall is quite thick and muscular, but at its apex it makes a turn and quickly reduces to the caliber of the histologically similar basal vas deferens. The epithelium facing the lumen of the penis in this region is strongly vermiculate. The outer spongy muscle layer of the penis seems continuous with the fibers of the penial retractor. Basal to the verge, the penial wall is thinner and internally thrown up into bifurcating and anastomosing longitudinal rugae. Basal to the level where the sheath leaves the penis, the penial wall is still thinner and externally ragged appearing because of the many irregular muscle bands passing to the genital atrium wall. Some anatomists might be tempted to refer to the apical portion of the penis as the epiphallus; but the use of that term here is not necessary. And further, as is often the case with this basically vague term, it would give no indication of function and would actually obscure homologies. The subject of penial homology is discussed in detail below.

Lehmann described and illustrated the genitalia of *Bulimus* (*Limicolaria*) *adansoni* Pfr. which since has been placed as a synonym of *L. kambeul*. His illustration, unfortunately, is not sufficiently detailed to

enable the author to make a positive statement in support of this reduction to synonymy, though there is nothing to indicate that it could not be *kambeul* that Lehmann had. He describes a unique "darmförmiges Organ" near the penis; this without much doubt is not part of the genital system but a slip of adjacent tissue — perhaps the body-wall. The ovotestis is shown, probably incorrectly, as a single mass of acini rather than the typical 4–5 smaller masses.

Four specimens from the Gold Coast were examined; one collected at Achimota in June, two at Labadi in July, and one at Nsawam in August, 1944. All specimens were collected by the author.

Measurements in millimeters of genitalia of three typical specimens: P — 12; 17, 16; PS — 7, 10, 9; PR — 7, 3, 10.5; VD — 23, 24, 21; V — 6, 9, 8; SD — 2, 3, 5; S — 17, 20, 19; FO — 16, 17, 18.

Limicolaria flammea (Müller)

Figs. 31, 32

The penis in this species peculiarly attains a gamma-shape and, like that of *L. kambeul*, its sheath is apically placed and tightly fitted, extending only slightly beyond the tip to embrace the very base of the short penial retractor which similarly inserts upon the right tentacular retractor. Sheath muscle elements pass onto the basal vas deferens forming a distinct enlargement which might be mistaken for a small epiphallus. Internally, the vas deferens in this region is much thicker walled than it is apically and it therefore might be presumed that this portion has an ejaculatory function. Basally the sheath enlarges slightly to pass over the swollen angle of the penis and then immediately terminates after making a second constriction. This gives an external appearance of the penis ending at the angle and the sheath extending in prepuce fashion considerably beyond it and at right angles to it. Wide, thin muscle bands originating in the sheath muscle, extend from a point near the very base of the sheath to the basal portion of the penis. Apically, the vas deferens is noticeably enlarged. The long slender free oviduct attains a diameter scarcely larger than the middle portion of the vas deferens. The spermatheca is a very large sacculate structure having both a terminal and a basal bulbous portion. In some specimens, the central constriction was more pronounced so that two globose portions were formed. The spermatheca duct is about the same diameter and half the length of the completely unmodified vagina. There is a deep genital atrium which appears to be directly continuous with the penis. As far as could be determined, there were no specific differences in the apical genital structures.

When the thin-walled penis sheath and the penis were cut open to determine the nature of the internal structures, a basically similar condition to that of *L. kambeul* was found. The verge, however, was more pronounced and situated at the angle of the penis, hence being responsible for the previously observed swelling in that region. Because of this more apical location of the verge, the rugate penial wall below the verge makes up the greater portion of the penial tube. Conversely, the portion of the penis above the verge, though vermiculate internally and otherwise similar to that of *kambeul*, is considerably reduced. There is little question that *flammea* and *kambeul* are quite closely related.

Four from a lot of ten specimens were examined; all were collected by the author in Weija, Gold Coast, in December, 1944. The uterus of one specimen contained forty canary-yellow, obovate (3x4 mm.) eggs. Their extremely thick, porcelain nature seems to preclude the possibility of ovoviviparity, which Robson (1912) suspected in an unnamed species of *Limicolaria* and *L. smithi*.

Measurements of genitalia in millimeters: P — 13, 12, 12, 12; Verge — 2, –, –, 1.5; PS — 7, 7, 7, 7; PR — 6, –, 7, –; VD — 15, 15, 17, –; V — 9, 9, 6, 10, SD — 4, 3, 3, 3; S — 15, 14, 20, 12; FO — 10, 10, 12, 11.

Limicolaria felina Shuttleworth

Figs 33, 34

Semper, 1873, pp. 142–143, taf. xii, fig. 1.

The penis sheath in this species is more basally placed so that the apex of the penis, the origin of the longer penial retractor and the base of the vas deferens are not obscured. Basally, the sheath is longer on one side than the other and its margin seems ragged with irregular muscle bands trailing down to thin points of attachment on the wall of the prominent genital atrium. The basal vas deferens is embraced by the uppermost portion of the sheath. The apical vas deferens is typical in that it is enlarged. In every case, the penial retractor inserts upon the right tentacular retractor. The unmodified vagina, which is conspicuously longer than the penis, narrows slightly towards its base. The free oviduct is long and of noticeably greater diameter than the vas deferens. Like the preceding species in this genus, the spermatheca consists of terminal and basal sacculate portions joined by a more narrow median portion. The basal portion, however, joins the vagina so broadly that a spermatheca duct, as such, is not apparent. No character of the apical genital structures appears to be peculiar to this species.

The thin-walled penis sheath and penis were dissected with the expectation that a condition similar to that of *L. kambeul* and *flammea* would be found. In the basal portions and in the formation of a verge, this actually proved to be the case; but apically, quite a different situation was found. Apparently the muscle layer of the apical portion of the penis has become so hypertrophied that the penial lumen has been seriously encroached upon — so much so, in fact, that it is not appreciably larger than that of the vas deferens. The apical penis thus consists largely of a thick, spongy mass of muscle strands which blend imperceptibly with those of the penial retractor. And this matting of muscle tissue, containing both longitudinal and circular muscle fibers, has altered somewhat the nature of the nearly centrally located verge. Instead of its being a more or less solid structure consisting of an outgrowth of the inner epithelium and the adjacent compact muscle layers, it is made up of this same epithelium and packed with a very loose, spongy muscle layer. In two of the three specimens examined, this verge is asymmetrical in that it is noticeably smaller and shorter on one side. This may be an artifact of preservation though it should be remembered that the sheath was similarly asymmetrical. Basally the penial tube is like that of the previously dissected limicolarias with the exception of the facts that internally it is thrown into numerous longitudinal, vermiculate ridges and externally it is nearly completely embraced by the sheath.

Without having first seen the penes of *kambeul* and *flammea*, these relationships would probably not have been correctly interpreted; for it appears as if the wall of the basal vas deferens, along with an apparently enlarged penial retractor, had greatly hypertrophied. The vas deferens thus seems to pass directly down into the verge and this latter seems to mark the apical termination of the penis proper. With the exception of the presence of an outer sheath, then, the penial components would seem to assume the relationships found in the land slugs *Hesperarion niger* and *Ariolimax columbianus* of western North America (Mead, 1943).

Semper illustrated and described very briefly the genitalia of *Achatina* (*Limicolaria*) *turbinata* "Reeve."[1] An examination of Semper's illustration does not make it possible to determine whether there exist tangible anatomical differences between the genitalia he describes and those described here for *felina*. Semper seems to have been "loop" conscious, probably through the fact that he was overly impressed by the conspicuously looped condition of the apical penis and basal vas

[1] Reeve's *Bulimus turbinatus* is a *Limicolaria* but Lea's *Achatina turbinata* is a *Pseudotrochus*. Pilsbry (1904–05) referred Reeve's figure to his *L. felina* var. *zebra*. There seems to be no way of determining whether Semper dissected typical *felina* or the variety *zebra*.

deferens of *A. panthera* (which he mistakenly refers to as *A. fulica*). He thus shows "*turbinata*" as well as other species with a more pronounced loop than probably actually exists. The rest of the genital system, except the unilobulate ovotestis, seems thoroughly within the bounds of *felina*. Though he does not mention it, his illustration indicates that the penial retractor makes its insertion on the tentacular retractor.

Three Gold Coast specimens were examined; two were collected by the author at Kumasi in November 1944 and one at Aburi (20 miles east of Accra) in October, 1944.

Measurements of genitalia in millimeters: P — 6.5, 6, 6; Verge — 1.5, 1.3, 1.7; PS — 5, 5, 4; PR — 8, 9, 9; VD — 15, 12, 10.5; V — 7, 8.5, 7; SD+ S — 11, 11, 9; FO — 6, 6, 7.

Limicolaria saturata capitellum Pilsbry

Figs. 35, 36

A paratypic series (46479) of five specimens (two very immature) from the Academy of Natural Sciences of Philadelphia was examined. These were collected in November, 1919, at Medje, Belgian Congo.

The sheath extends further down than in any of the previously examined species of this genus. Actually, its basal limits are nearly completely obscured by many thin muscle bands originating in the sheath and passing to points of insertion on the penial prepuce and the wall of the genital atrium. In two of the specimens, the long penial retractor inserted upon the right tentacular retractor; in the third specimen, it inserted on a vertical sheet of tissue, the sagittal myoseptum (discussed below). The immature specimens were not examined. The vas deferens leaves the sheath close to its apex and, without approaching the peniovaginal angle, it passes to an apical swollen portion that joins the free oviduct.

The tubular, unmodified vagina is approximately twice as long as the penis sheath and seems to bifurcate to form the free oviduct and the shorter spermathecal duct. This latter gives rise to the spermatheca which consists of a basal bulbo-sacculate portion narrowly joined to an apical clavo-sacculate portion.

The fairly thick-walled sheath was cut to expose a penis whose proportions are very similar to those of *L. felina*. However, the spongy mass of muscle strands, that makes up the penis apical to the centrally located verge, and the tubular portion basal to the verge are proportionately longer than in *felina*. But aside from this, the very different sheaths make it easy to distinguish these two closely related species.

An abbreviated penial retractor and a much larger verge in the very closely related *L. ussuwiensis* set that species off as still different.

Inasmuch as the second specimen dissected was abnormally attenuated, apparently during preservation, the measurements in millimeters, of only two specimens are given here. The first figure in each case refers to the specimen illustrated. P — 6, 5; PS — 6x3, 5.5x2; PC — 2x1, 2; Verge — 1.5, 1; PR — 16, 10; VD — 18, 21; V — 12, 11; SD — 3, 3; S — 15x1–4, 14; FO — 6.5, 8; AG — 14, —.

Limicolaria ussuwiensis Kobelt

Figs. 37, 40

There were examined six specimens collected for the Institute of the Belgian Congo National Parcs, labeled "Burunga (Mokoto), Belgian Congo. Mission de Witte No. 288." In all six specimens, the very short penial retractor inserted upon the diaphragm; and in all but two of these, the insertion was quite near the anterior rim of the mantle. Though the penial sheath is, in general, more slender, it still is very similar to that of *L. saturata capitellum* in that it covers all but the very basal portion of the penial tube. The vas deferens is swollen apically and is typical of the genus as it does not reach the peniovaginal angle. Basally, the vagina tends to be enlarged to such an extent that the genital atrium is obscured and the penial prepuce is encroached upon. In this respect, it is in contrast with *L. flammea* (Fig. 32). The free oviduct is approximately the size of the vas deferens. There occurs between the two sacculate portions of the spermatheca, not a simple constriction but a very definite isthmus which is approximately the length of the spermathecal duct. The form of the spermatheca as depicted in Fig. 40 is consistent throughout the series and is probably typical for the species.

Cutting the sheath, which is slightly thicker in its apical portions, revealed a penis of the type found in *Limicolaria felina, saturata capitellum* and *Limicolariopsis kivuensis*. The reduced muscular network of the apical penis, however, emphasizes the fact that the verge in this species is larger than in any of the others. Longitudinal vermiculations mark the lining of the penis basal to the verge.

Diagnostic characters of this species, then, rest in the penial retractor, verge, vagina and spermatheca.

Measurements of genitalia in millimeters (the illustrated specimen is the first one listed):

P	5	—	—	—	5	—
PS	8	6	8	7	6.5	7
PR	3	2	4	2	2.5	2.5
PC	2	—	—	—	—	2
Verge	3	—	—	—	3	—
VD	16	19	19	14	13	13
V	11	12	9	15	10	11
SD+S	14	10	15	12	16	15
FO	8.5	8	8	8	6	7
AG	20	7	9	15	10	16

Limicolariopsis kivuensis (Preston)

Figs. 38, 39

A single specimen of this species, (MCZ 77059) collected on the "trail from Burunga, Belgian Congo", had been dissected and reported upon by Clench and Archer (1930). The carefully removed genitalia, however, were not figured by them but are shown here.

The penial tube is entirely enclosed within the thin-walled sheath with the exception of a very short basal piece, the prepuce, close to the shallow genital atrium. The sheath was rather acutely bent in its basal one-third, as shown in the figure. This bending has been observed in preserved specimens of other species and though it is not felt here that this is a naturally occurring feature, it is not forgotten that *Limicolaria flammea* (Fig. 32) has a consistently angulate, diagnostic apical penis and sheath. Freshly killed material is actually needed to determine for certain the nature of this character. Immediately after the penial retractor leaves the confines of the sheath, it becomes very narrow and long. It clearly inserts upon the diaphragm. Muscle elements from the sheath pass out on the basal vas deferens obscuring its point of departure from the sheath. The vas deferens does not even approach the peniovaginal angle but enlarges slightly before joining the free oviduct. Like those of *Limicolaria*, the prostatic acini are noticeably larger than those of *Achatina* and *Archachatina*. The vagina also is similar to those of the examined species of *Limicolaria* in that it is very long (one and one-half times the length of the penis sheath) and tubular. Its apparent angulate nature is probably an artifact of preservation. The similarity to *Limicolaria* is carried still further, for the spermathecal duct has two distinct sacculations. The free oviduct is not as long as the sheath and is only slightly larger in diameter than the vas deferens.

Upon cutting the thin-walled sheath, which was very thin in its basal portions, it was seen that the relationships of the penial com-

ponents were like those of *Limicolaria felina, saturata capitellum* and *ussuwiensis*. The nearly centrally located verge is not as large as in this last species but it is definitely larger than in either of the other two. The basal penial retractor and the loose matting of muscle fibers of the apical penis are so intimately intermingled that the retractor seems to be basally very massive and to have a very broad origin on and in the verge. The lining of the basal portion of the penial tube seems to be thrown up into dense, depressed papules.

Clench and Archer (1930) point out the great similarity of this species to *Achatina* (= *Euacthiops*) *loveridgei* on the basis of the penes; but as indicated in the discussion of this latter species, the penis of *loveridgei* was not properly interpreted. In view of this re-examination, their relationship is without question quite distant, a great similarity in the flared lip of their shells notwithstanding. On the other hand, their conclusion that *Limicolariopsis* and *Limicolaria* are closely related is a thoroughly sound one. And as a matter of fact, this anatomical study of *Limicolariopsis kivuensis* shows that this species apparently is more closely related to the three species of *Limicolaria* mentioned above than any one of these latter is to either *Limicolaria kambeul* or *flammea*.

Measurements of the genitalia in millimeters: P — 10x3; PS — 14.5; Verge — 4; PR — 28; PC — 2; VD — 25; V — 20; FO — 9.5; SD + S — 22; AG — 12.

Pseudotrochus turbinatus mucidus (Gould)

Figs. 42, 43, 44, 46

Three rather badly dehydrated specimens preserved in alcohol were soaked twenty-four hours in an 0.8% solution of trisodium phosphate before they were examined. These were collected by Joseph C. Bequaert near Dobli Island, Liberia, on April 12, 1944.

A very noticeable reduction in the vascularization of the roof of the pulmonary chamber was found. As Clench and Archer (1930) report, a similar condition is found in *Achatina loveridgei*, though not to this great extent.

Of the three specimens, two had been removed from their shells and one was left intact. The larger of the first two was dissected (Fig. 43) and it was found to be gravid with embryos. The penis (Fig. 42) is clavate, hollow, and with the exception of the very abbreviated prepuce, the penial tube is completely embraced by the thin-walled sheath. The short penial retractor is broad at the point of origin and attaches to the right tentacular retractor. A subterminal junction

occurs between the penis and the very slender basal vas deferens. The latter apically folds back upon itself, leaves the sheath in its basal two-fifths, and passes to the peniovaginal angle. At its junction with the spermoviduct, there is an asterisk-like, lobulated gland whose possible function is discussed below.

In the middle of the tubular, essentially unmodified vagina, is a transverse constriction that may well be an artifact produced when the animal was killed. The spermatheca duct is only slightly over half the length of the vagina and the free oviduct is scarcely one-fifth its length. Eight fully formed embryos, 4x5 mm., extend from the free oviduct to the albumen gland, *i.e.* throughout the entire length of the apical and basal parts of the uterus. Each has a well calcified shell of two and one-half whorls covered by a thin, transparent membrane (Fig. 44). A talon is present and is typical of the other achatinids examined.

The smaller specimen was very immature and no significance could be obtained from its examination except for the fact that the sheath was short and the penis projected apically well beyond it as it did in the immature specimen of *Arch. osborni afromontana*.

The third specimen was removed from its shell and though it was mature, as evidenced by the presence in its oviduct and uterus of several homogeneous albumen masses as large as the embryos in the first specimen, the sheath-penis relationships (Fig. 46) were like those in the immature specimen. The sheath did appear contracted, though it is not possible in the absence of fresher material to determine the significance of this variation nor to establish accurately the basic genital plan from which relationships can be drawn. Some light seems to be thrown on this by the study of the single immature specimen of *P. interstinctus insignis* (*vide infra*). Only slight differences were found in the other structures.

Measurements of genitalia in millimeters (the two specimens are listed in order of examination): P — 7, 9.25; PS — 9, 5; PR — 5, 8; VD — 12.5, 12; BV — 4, 4.5; AV — 4, 4.5; FO — 1.5, 3.5; SD —4.5, 2.5; S — 3.5, 2.75; AG — 10.5x3, 6.

Pseudotrochus interstinctus insignis (Pfeiffer)

A single specimen collected on April 12, 1944, near Dobli Island, Liberia, by Joseph C. Bequaert was examined. The genitalia were so immature and attenuate that they were practically valueless in this study. The penis sheath, however, was short and only one-third the length of the attenuate penis. This would seem to lend support to a

presumption that the specimens of *Pseudotrochus turbinatus mucidus* with the shorter penial sheath (Fig. 46) are more normal than the one with the longer penial sheath (Fig. 43). Dissections of other achatinines have shown that the immature specimens often tend to have a short penis sheath even when it is normally long in the adults. But these observations still leave unexplained the reason for the apparent dimorphic condition of the sheath in *P. turbinatus mucidus*.

SURVEY OF THE LITERATURE

An exhausting but probably not completely exhaustive search of the literature has been made in order to determine the extent to which the genitalia of the Achatinidae have been examined and illustrated. The search yielded illustrations of nineteen species and subspecies of which six have been re-examined, re-illustrated and re-described above in the light of a more clear understanding of the genital components and interrelationships. The nonexistence or unavailability of preserved material has prevented a similar rechecking of the remaining thirteen species and subspecies. Therefore in order to make the record as complete as possible, it has been necessary to make outline copies of the original illustrations for reproduction in this present paper. These original illustrations were so variously executed that it was thought advisable to reproduce them in such a manner that all would be similarly arranged and brought to approximately the same size (Figs. 54–63). A study, then, of such a series of illustrations, in conjunction with the original illustrations which the author has contributed, will not only permit of more accurate drawing of homologies, but the relative taxonomic value of the genital system can be more nearly ascertained. In this process of re-drawing, every precaution was taken to preserve the same dimensional ratios as appeared in the original illustration. Here and there, however, liberties were taken in incorporating characters where they were clearly described in the text but not or poorly shown in the originals. These are accurate, then, only in so far as the original investigators were accurate in their observations and illustrations.

There is presented below, with brief annotations, a list of these thirteen species and subspecies whose genitalia have been illustrated or discussed in the literature.

Achatina (Achatina) dammarensis Pfeiffer

Fig. 54

Degner, 1922, pp. 37–38, figs. 12c, 13.

We have in this species apparently a genuinely unique form in the male genitalia inasmuch as the penis and vas deferens are reported to be peculiarly bulbous in the region where they join each other and where the penial retractor has its origin. On the other hand, it is thoroughly possible that severe contraction of the penial sheath at the time the specimen was killed has produced these swellings as artifacts. Degner describes in detail the external and internal anatomy of the basal structures. He describes a wide fold on the inner wall of the penis which is presumed to be a stimulatory organ (Reizorgan). The vagina is divided into basal and apical portions. The penial retractor was found to make its insertion on the floor of the lung, on the strength of which he incorrectly links this species with *Limicolaria vanattai* and *Archachatina simplex crawfordi*. The significance of variations in the insertion of the penial retractor is discussed below.

Achatina (Achatina) schweinfurthi v. Martens

Fig. 55

Pilsbry, 1919, pp. 72–73, figs. 31, 32.

Pilsbry's photographic plate of the genitalia of this species gives quite a fair idea of all the basal structures except the length and form of the spermatheca. It was hoped that the original specimen could be re-checked to determine this but efforts to locate it were not met with success. Examination of other species in this genus has shown, however, that in general the spermatheca is coextensive with the free oviduct and contiguous with the basal spermoviduct. With this thought in mind, there is indicated by a dotted line an attempt to approximate its probable dimensions.

The term "epiphallus", which Pilsbry used in referring to the basal vas deferens, is misleading.

Achatina (Achatina) zebra zebra (Bruguière)

Semper, 1874, p. 144.
Pilsbry, 1904–05, p. xiii.

Semper did not illustrate this species but described its genitalia in the most brief and general terms, presenting as the only significant

character the fact that the spermathecal duct was short. Pilsbry also referred to this character.

Achatina (Achatina) zebra obesa Pfeiffer

Fig. 56

Robson, 1921, p. 256, fig. p. 257.

Robson described in considerable detail the genitalia of "*Cochlitoma zebra* var. *obesa* (Pfeiffer)" which, like the parent species, reportedly possessed a short spermathecal duct. He was in error, however, when he referred to the free oviduct as the "vagina" and to the vagina as the "common duct of vagina and spermatheca." The penis sheath was found to be "complete" and the penial retractor "a branch of the right ocular band." It seems apparent from his findings that one of the two specimens he had ("z_2") was an attenuated immature specimen. His reference to an "anomalous condition" of the vas deferens (p. 262) in that specimen, therefore, is probably not a valid one.

Achatina (Achatina) zebra fulgurata Pfeiffer

Fig. 57

Robson, 1921, p. 262, fig.

Pfeiffer (1851) originally described this as a new species of the genus *Achatina*. Pilsbry (1904–05) relegated the species to the genus *Cochlitoma*. Robson retained it in the genus *Cochlitoma* but like his fellow British predecessors, considered it a subspecies of *zebra*. He was able to show, on the basis of his anatomical study of two individuals, differences between this and "var. *obesa*" in the length of the free oviduct (which he mistakenly calls the "vagina") and the spermathecal duct. His findings led him to "conclude that the present concept of the genus *Cochlitoma* is unsound." Connolly (1939) avoids the issue completely and cautiously takes the classification of Melvill and Ponsonby.

If the anatomical differences between *obesa* and *fulgurata* prove constant, and if these two are still to be considered mere subspecies of *zebra*, then there exist greater differences between them than between any other subspecies so far examined.

Achatina (Lissachatina) lactea Reeve

Fig. 59

Bacci, 1939, p. 337, fig. 2.

In this species, Bacci has made an even less correct interpretation of the structures than he did in *fulica hamillei* (*q.v.*). To the fact that he was unable to find a talon, which unquestionably is present, he assigned the absurd reason, "In questa specie il condotto ermafrodita non dà luogo alla formazione di un diverticolo." The greater length of the vas deferens is given undue significance. The nature of the penis is completely confused not only because he fails to distinguish between it and its sheath (though he implies it is completely covered by the sheath), but he creates out of the swollen basal portion of the penial retractor "un epifallo piriforme." The characters of the basal female conduit seem to be significantly different from those of *fulica*.

Archachatina (Tholachatina) granulata (Krauss)

Fig. 58

Semper, 1874, p. 143, taf. xii, fig. 2.

It is apparent from Semper's illustration that what he refers to as the loop of the vas deferens is actually the apical penis and the adjacent basal vas deferens. These project considerably beyond the confines of the penis sheath and, along with the greater length of the vagina, are in contrast with the other illustrated species put in the genus *Cochlitoma* by Pilsbry. It was this contrast that stimulated Robson (1921) to point out that *granulata* "does not fall into line in the character of its penis sheath" and was used by him to support his contention that the genus *Cochlitoma* was of questionable status. Semper considered the genitalia similar to those of *Archachatina marginata*.

Burtoa nilotica nilotica (Pfeiffer)

Reynell, 1906, p. 197, pl. 17, fig. 2 a, b, c.

The typical form of this species has been examined and illustrated by Reynell. He shows the conspicuously slender penis somewhat enlarged at its apex and projecting with the slightly smaller basal vas deferens in loop fashion a short ways beyond the apical rim of the apparently quite thick sheath. He is inconsistent, however, in indicating the length of the vagina, for in one of his figures it is longer than

the penis and in another it is considerably shorter. Just the reverse is shown in the length of the spermathecal duct. The spermatheca is shown as a large, irregularly sacculate structure; but he reports that it varied in the "pregnant and non-pregnant animals." He reports that the penial retractor inserts "distally on the diaphragm." In two of his specimens, he found 154 eggs each "contained in a calcareous shell." No free embryos were found.

Burtoa nilotica obliqua (v. Martens)

Fig. 60

Pilsbry, 1919, p. 81, fig. 34.

In spite of Pilsbry's feeling that Reynell and Pollonera had different subspecies than the one he examined (*obliqua*), the figures of the three authors compare very favorably. Pilsbry's illustration of the basal genital structures of this subspecies is reproduced here as there are inconsistencies in the illustrations of Reynell and misinterpretations in those of Pollonera. In a second diagram, Pilsbry shows the penial retractor originating all along the portion of the vas deferens embraced by the sheath; this, of course, is not unique (*Cf. e.g.* Figs. 11, 17). The spermatheca is shown as small and globose and the penial retractor is reported to insert on the diaphragm.

Burtoa nilotica minor Pollonera

Pollonera, 1909, p. 197, pl. 19, figs. 6, 7.

Though Pollonera does not discuss the genital structures of this subspecies, he has illustrated them. In his two figures, he shows at the apex of the penial sheath (which he calls the "pene") some peculiar structures. To one who is acquainted with achatine genital anatomy, it is easily seen that what he terms the "flagellum" is actually the basal stub of the penial retractor. That which he terms the "retrattori" is the thin penial artery, with its adjacent muscle fibers coming from the ganglionic region and passing into the inner walls of the sheath via its apex. The remaining, and unlabeled, structure in his illustration is obviously the loop formed by the apical penis and basal vas deferens. The spermatheca, labeled the "borsa copulatrice", is globose and like that of *obliqua*.

Limicolaria vanattai Pilsbry

Fig. 61

Pilsbry, 1904–05, p. xi, pl. 65, fig. 42.

In his discussion, Pilsbry points out that the penis sheath envelops the entire penis, the basal portions of the vas deferens and the retractor muscle. He describes the penis as "thick and short" though he does not attempt to show it in his illustration. The spermathecal duct is conspicuously longer than the free oviduct and the sheath embraces the vas deferens only in its most basal portion in the region of the apical penis. The penial retractor attaches to the "lung floor or diaphragm."

Pseudotrochus alabaster (Rang)

Fig. 62

Semper, 1874, p. 145, taf. xii, fig. 3 [not fig. 1 as he reports in the text].
Pilsbry, 1904–05, p. xi, pl. 1, fig. 1.

This species is conspicuous in that the vagina is long, the spermathecal duct is very short and the robust penis projects considerably beyond the short, basal penial sheath. In these respects, the genitalia are similar to those of *A. achatina, P. turbinatus mucidus* and *P. interstinctus insignis* and further substantiates the thesis that the sheath is normally short in this genus. The penial retractor is reported to connect with the columellar muscle.

Atopocochlis exarata (Müller)

Fig. 63

Furtado, 1888, pls. 2, 3.
Pilsbry, 1904–05, p. x, pl. 1, figs. 8, 9.

Furtado has shown the genitalia of this species in fair detail; Pilsbry has reproduced his illustrations exactly. The penial retractor is reported to make its insertion on the columellar muscle. The basic plan of the genital system is not tangibly different from that of the examined species of *Pseudotrochus*. This lends significance to the fact that some authors consider *Atopocochlis* congeneric with *Pseudotrochus*.

THE BASIC PLAN IN PENIAL ANATOMY

A comparative study of the genitalia of the several species in the subfamily Achatininae has revealed that the most complex and taxonomically most significant achatinine genital structure is the penis with its sheath and retractor. It was found that in spite of striking differences, all penes could be reduced to a common, basic plan, the establishment of an understanding of which permitted for the first time a correct interpretation of the intricate, variable and heretofore apparently indecipherable relationships of the penis and its attendant structures.

In the material examined, the genitalia of *Achatina fulica* are very nearly the least specialized and therefore will serve as a good example to illustrate this basic plan. Further research may possibly show that these are not prototypic in this group. At present, however, all others that are known can be derived from a plan similar to the one demonstrated in this species. With the help of the schematic and idealized illustration in Figure 41, then, let us examine the basal portion of the male conduit in *A. fulica* to get an understanding of the basic interrelationships of its component parts. With this established, it will not be difficult to homologize them in the other species. As will be seen in the conclusions, where each species is discussed in the light of all of its significant characters, homologizing from this basic plan will help to establish a concept of phylogeny in this group which seems entirely impossible from the study of the shells alone.

First of all, it helps to keep in mind that the male conduit, basal to the spermoviduct, is essentially a long, hollow tube which is apically reduced to form the vas deferens and basally enlarged to form the penial tube. The latter is able to pass out in part or in its entirety as the intromittent organ during copulation. At the junction of the apical and basal parts, a slip of musele arises from the outer muscular wall of the conduit and passes normally in this group to the right tentacular retractor, though as explained below, it occasionally inserts at other places. The principal modification in this conduit is the formation of a penis sheath. It will be seen that the sheath (PS) is not a separate entity but merely a continuation, a doubling back and a thickening of the outer muscular wall of the penis (OP) and the vas deferens (OV). As it passes apically then, it embraces the basal vas deferens a second time and completely surrounds the penis including the basal portion of its retractor (PR). In this process, the penial artery (PT, *Cf.* also Figs. 7, 50) is not embraced but pushed apically so far that it must make a hairpin loop in order to reach the inner wall of the sheath where it breaks up into smaller vessels. This artery

arises near the circumesophageal nerve ring as a branch of the right cephalic artery which, in turn, is a branch of the anterior aorta. Because this artery is surrounded by a thick band of connective tissue, it is quite prominent and in some cases has confused investigators. Pollonera's reference to it as a "retrattori" in *Burtoa nilotica* is a case in point. Other investigators, who stopped too soon in their dissections, were misled by the prominence of the penial sheath and have erroneously referred to it as the penis proper. This has led to some gross misunderstandings as to the relationships of certain species.

Internal to the outer muscular layer of the vas deferens (OV) is an inner more or less spongy, muscle layer (IV) and an epithelial layer (EV) which are continuous with those of the penis (IP, EP). The same two layers are seen to make up entirely the walls of the genital atrium (GA) and the unensheathed basal portion of the penial tube (PC). This latter has been frequently referred to in related groups as the "penial prepuce." The nature of its walls indicates that it is a direct extension of the genital atrium and it might therefore be considered a "penial atrium." This term, however, is no better than the other one as far as indicating what its true function is in copulation. The term "basal penis" has the right connotation but it would obviously lead to ambiguities. It is with some reluctance, then, that the term "penial prepuce", or simply "prepuce" has been used in this paper. A very pronounced constriction occurs in the penial tube at the base of the sheath; hence there is a definite demarkation between penis and prepuce. The much more delicate epithelial layer of the penis further emphasizes the difference in these two structures. Externally, however, the sheath often appears to pass all the way to the atrium. The reason for this is found in the fact that a variable number of muscle bands (MB), that have their origin in the sheath, pass basally and insert in many places on the prepuce and the genital atrium. Connective tissue (CT) also adds to the illusion. Often these must be cut away to determine the basal limits of the penial sheath.

In the achatinines that are known anatomically, the deviations from this basic penial plan seem to fall into six definite groups. The first, characterized by *A. fulica*, which has a very slender penis completely enclosed by a thick walled sheath, also includes the closely related *A. iredalei*, *zanzibarica*, *loveridgei* and *albopicta*. The penes in the second group are also short and confined to the sheath but they are quite robust. This group includes *Arch. osborni afromontana* and *Arch. simplex crawfordi* and apparently *A. zebra* and *A. schweinfurthi*. In the third group, to which belong *Pseudotrochus turbinatus mucidus*, *P. interstinctus insignis*, *A. dammarensis*, *Burtoa nilotica*, *Arch. meadi* and *Arch. granulata*, there is a definite tendency toward elongation

of the penis beyond the confines of the sheath. Pronounced elongation of the penis is demonstrated in the fourth group by *A. reticulata, A. glutinosa, A. layardi* and finally *A. panthera*. This tendency is carried to the extreme in the fifth group with the formation of a very robust, muscular penis which extends considerably beyond the sheath. This group includes *P. alabaster, Atopocochlis exarata, Arch. degneri, Arch. marginata, A. achatina* and *Arch. bicarinata*. In the sixth group, however, quite a different trend has taken place. In *Limicolaria kambeul* and *L. flammea*, the penis proper is completely surrounded by the sheath; but the prepuce has become so greatly elongated that the sheath appears to be apically situated. Further, there arises at the junction of the penis and the prepuce (which is an area of constriction in *fulica*) a basally directed, circumferential outgrowth of the inner muscle layer and the epithelial layer thus forming a distinct verge or penis papilla. In *L. felina, saturata, ussuriensis* and the obviously closely related *Limicolariopsis kiruensis*, the penis proper has become obscured through the hypertrophy of the middle muscle layer. This has not only reduced the lumen of the penis to a narrow passage, hardly larger than that of the vas deferens, but has formed a packing between the walls of the verge to make it a more pronounced structure. Actually, before the penis sheath is cut, the genitalia of members of this group look superficially quite similar to those of the first two groups above — hence the need for careful dissection of the penis itself.

INSERTION OF THE PENIAL RETRACTOR

Pilsbry (1904–05) found that the penial retractor of his *Limicolaria vanattai* attached to the "lung floor or diaphragm" and from this assumed that this character was typical for the genus. He also found a similar attachment in *Cochlitoma* (= *Archachatina*) *crawfordi*. Reynell (1906) found the same character in *Burtoa nilotica* and Pilsbry (1919) supported his observation by finding it in *B. nilotica obliqua*. On the strength of the fact that this character was found in *Achatina dammarensis*, Degner (1922) attempted to link this species with the others above. It is significant that each of these four species is in a different genus and, as far as the genital anatomy is concerned, is quite distinct from the others. This suggests immediately that caution should be exercised in assigning any taxonomic value to this character and that an extensive investigation is indicated so that its true value can be ascertained.

Though it was not possible to undertake such an investigation in the present study, a great deal of light has been shed on this general problem. In order to make as understandable as possible the complex

factors apparently responsible for the great variation in the attachment of the penial retractor, there has been prepared in Fig. 49 an idealized stereogram, basically typical of all genera studied, which is exaggerated in some dimensions to emphasize relationships.

First of all, it should be understood that the *origin* of the penial retractor (PR), as Hoffmann (1922, p. 521) has shown in his embryological study of *Limax maximus,* is on the apex, or near apex, of the penis (P). The *insertion,* then, will be found at the opposite end. And typical of insertions, it demonstrates greater variability in its attachment. This point frequently has been confused in the literature.

When the mantle (M) is cut away, in dissecting a specimen, the lung or pulmonary cavity is exposed. The muscular lung floor or diaphragm is traversed, from posterior to anterior, by the large, prominent anterior aorta (AA). Well before the anterior thickened rim of the mantle (AM) is reached, this aorta passes ventrally through the diaphragm to the ganglion masses where it gives rise to a number of arteries including a fairly large one to the penis. This penial artery, as explained in the discussion of penial anatomy, has been confused with the penial retractor. In examining the diaphragm lying to the left of and anterior to the anterior aorta (LD, LD) it is found to be muscular but very thin-walled. In contrast, the diaphragm lying to the right of and posterior to the aorta (RD) is much more muscular and approximately twice as thick. It was not understood why the anterior aorta seemed to rest in a very marked depression between these two sections of the diaphragm until the haemocoele (RH + LH), or main body-cavity, was exposed. A very definite vertical sheet of muscle and connective tissue (SM), oriented in a postero-anterior direction, was found to connect the diaphragm, immediately below the anterior aorta, with the giant, ventral columellar muscle (CM) hence dividing the haemocoele into right (RH) and left (LH) portions in this region of the body. This sagittal myoseptum, as it will be called, is of highly variable nature, for it may terminate abruptly with a considerably thickened edge at the level where the anterior aorta passes ventrally, or it may continue anteriorly to the peniovaginal angle and thereby put the penis and vas deferens (VD) in the left haemocoele with the crop and odontophore, and the entire female conduit by itself in the right haemocoele. If it does extend this far anterior, the right tentacular retractor (TR) is diagonally traversed by the sagittal myoseptum. Modifications of this have been found wherein this myoseptum passed more and more strongly toward the right until it passed not between penis and vagina but transversely over the lower portion of the spermoviduct until all of the basal genital structures rested in the left haemocoele with the crop.

Posteriorly the sagittal myoseptum gradually breaks into separate muscle bands that become smaller, shorter and more sparse. Shortly posterior to the last band, the right tentacular retractor joins with the left tentacular retractor (TL) which latter has already joined with the combined left (OL) and right (OR) retractors of the odontophore. These four muscle bands then, join the columellar muscle in its most posterior portions to form a single contractile unit. It should be borne in mind that the tentacular retractors not only attach to the two tentacles on their respective sides but to several other places on the head and neck regions.

Springing from the sagittal myoseptum is another nearly vertical sheet of muscle and connective tissue, the transverse myoseptum (TM). This connects dorsally, in an arc, along the left diaphragm and finally makes a terminal attachment in the region where the diaphragm attaches to the columellar muscle. A separation of the left haemocoele into an anterior portion, containing the crop, and a posterior portion, containing the stomach, is thereby effected. As both myosepta are quite muscular and are vertically oriented, it is very possible that they supplement the work of the diaphragm.

By far the majority of the achatinid specimens examined had the insertion of the penial retractor on the right tentacular retractor either at a point (A) anterior and to the left of the sagittal myoseptum; or, when the myoseptum was shorter or turned more sharply to the right, at a point (B) further up the right tentacular retractor and therefore sometimes to the right of the myoseptum. This, without much doubt, is the *normal* type of insertion for this group.

In one of the specimens of *A. simplex crawfordi* the insertion of the penial retractor was found to be perfectly normal. In the other, it was such that some of the fibers fused with the right tentacular retractor and the rest fused with the adjacent portion of the sagittal myoseptum (at C). A small piece of this myoseptum remained at the apex of the penial retractor when the genitalia were removed (Fig. 27, SM; *Cf.* also Fig. 25). A large specimen of *A. reticulata* (Fig. 13), went one better by having apical fibers passing not only to these two points but to the columella (at D) as well. For a still different combination, one of the paratype specimens of *A. leucostyla* (= *fulica hamillei*) had an apically bifurcated retractor that inserted on the right tentacular retractor and on the columella. And on the other hand, single specimens of *A. iredalei* and *L. saturata capitellum*, from series of otherwise normal specimens, had insertions entirely upon the sagittal myoseptum (at E).

Working still further dorsally, one of six specimens of *A. zanzibarica* had a retractor that inserted on the right tentacular retractor, the

sagittal myoseptum and on the ceiling (at F) of the diaphragm or lung floor; or to be more accurate, on the ceiling of the left haemocoele. Several species had one or more individuals with retractors that passed vertically along the left side of the sagittal myoseptum, over the crop and inserted centrally on the diaphragm; these are *A. zanzibarica, loveridgei, Arch. simplex crawfordi, meadi, osborni afromontana, Limicolaria ussuwiensis* and *Limicolariopsis kiruensis*. In all six specimens of *L. ussuwiensis* the insertion was on the diaphragm but in four cases the insertions were anteriorly placed very close to the junction of the left diaphragm and the mantle (at G). Still greater anterior progress was made in *Arch. osborni afromontana*. Two of the six specimens examined had insertions centrally on the diaphragm and four of them had insertions on the body-wall (BW) anterior to the diaphragm and the anterior lip of the mantle (at H).

From these observations, the following conclusions can be made relative to the insertion of the penial retractor: (1) The sagittal myoseptum interferes with the normal insertion of the penial retractor by acting as a physical barrier. This interference may cause the retractor to insert upon the myoseptum itself or be deflected over the crop to the diaphragm, or it may cause a splitting of the terminal retractor with slips passing to two or three different points of insertion. (2) Orientation of the penis anlage undoubtedly predisposes a certain type of insertion. The short, often anteriorly directed penis in *Arch. osborni afromontana* may be a case in point. (3) Deviations from the normal insertion have occurred sporadically a good many times in the Achatininae for the reasons indicated above; and actually, they are by no means limited to the subfamily Achatininae, for Connolly (1925), in his discussion of the subulinine genus *Pseudoglessula*, points out that he found the penial retractor attached to the "retractor of the right tentacles" *i.e.* "the columellar muscle, as in so many of the Achatinidae and not from the diaphragm, as Pilsbry [1919] states that it does in *Ps. stuhlmanii* (Mts)." These deviations cannot therefore be considered of taxonomic significance, though there remains the possibility that when very large series of *Arch. osborni afromontana, L. ussuwiensis* and perhaps others are examined, they may be found to be secondarily consistent in their deviations because of an inherent consistency in the predisposing factors. (4) Pilsbry (1904–05, p. xi) has assumed that the diaphragmatic insertion in this group is indicative of a "true" penial retractor and a "normal insertion" whereas the insertion on the "right ocular retractor" is a "secondary" one. The present investigation does not support this assumption. On the contrary, it indicates that just the reverse is more likely the case.

COPULATION AND COPULATORY ANATOMY

Most of the achatinids studied possess a simple tubular penis which may be short as in *Archachatina osborni afromontana* or long as in *Achatina achatina*. In either case, it is not difficult to imagine how the intromittent organ is formed during copulation or what is extroverted in the process. And even in *A. panthera* with its very long, sinuate vagina, the mechanics of copulation would seem fairly simple. It is quite different in *Achatina fulica, iredalei, zanzibarica, loveridgei* and especially *albopicta*, however, as the extremely small, thin penis and the very thick, muscular sheath give no idea as to what takes place in extroversion. It was soon apparent that the answer would be found only in witnessing the actual extroversion process itself.

The opportunity very fortuitously presented itself at 10:30 p.m. on June 27, 1948, when the author made his final evening check of the terrarium containing two specimens of *A. fulica hamillei*, three of *A. iredalei*, three of *A. reticulata* and one of *A. fulica rodatzi*. All specimens were actively crawling about or feeding on lettuce and carrot. The single specimen of *rodatzi* from Zanzibar, that hereinafter will be referred to as "A", was seen to be approaching one of the *iredalei*, which hereinafter will be referred to as "B", from the rear and to be moving at least twice as fast as the rest. As it contacted the posterior portion of the foot of "B", the rhinophores, which were fully extended and forming about a 90° angle, were brought very close to the shell of "B". In this fashion, they skimmed over the surface rising and lowering with each elevation and depression as "A" progressed anteriorly over the shell of "B". The appearance was very much like that of a bull that has its head and horns lowered for a charge. The head of "A" was seen to swell very noticeably. As "A" continued to move forward, now more slowly, the genital atrium completely everted as did the penial prepuce. The orifice leading into the vagina was apparent and the whole structure looked not unlike the folded hand with the index finger extended. "B", however, did not respond to this approach and "A" moved from side to side several times almost as if in confusion, and then slowly crawled away. The genital atrium and penial prepuce were gradually invaginated again.

But "A" seemed charged with persistence. It next moved over to the shell of a giant *A. reticulata* — again approaching it from the rear. As it neared the anterior end of the shell, once again the atrium and penial prepuce became more and more extended and the rhinophores were held close to the shell and at the same angle. Again, there was no response and the withdrawing action of "A" was the same as before.

A smaller specimen of *A. fulica hamillei* from Kenya, which herein-

after will be referred to as "C", was then approached head on. The movements of "A" did not seem purposeful but it moved to one side of "C" and after an irregular course approached "C" from the rear as it had the others. The same response was noted in its basal genital structures as before. At the same instant, "C" showed an identical response and began to rise upright as "A" approached the neck region, just as it had done with the others. As "A" buried its head deeply between the neck and the anterior rim of the shell of "C", the latter rose still higher and more vertically off the terrarium floor. "A" seemed to be half rasping, half caressing the neck region of "C" and at the same time, "C" was beginning to lean further and further back onto the dorsally situated "A". Each individual had the genital atrium and the penial prepuce fully extended. "C" showed a great deal of activity by way of contracting and extending the four tentacles and the anterior region of the head in general.

Finally "C" began to turn to its right so that "A" brushed against its expanded atrium and prepuce more and more as it moved up higher and higher on the neck region of "C". Reciprocally, "A" turned slightly to its left so that its corresponding genital structures were also being brushed continually against the neck region of "C" as they both passed each other in wider and wider sweeping motions of the head and neck. It was now quite apparent that the everted genital atrium and penial prepuce were functioning as a stimulatory organ[1].

As the activity became more and more pronounced, the genital regions came closer and closer together. Finally, a large, very clear but yellowish drop of very viscous fluid was produced simultaneously at the tip of each stimulatory organ (thus coming from the male system) and the next time the individuals brushed against each other, these drops were each deposited close to the mouth of the other. With this, the two individuals tightly appressed their stimulatory organs together and simultaneously contracted the head and neck regions so that a fair amount of altitude was lost. There was a very definite high rate of internal activity for the first minute, at which time the extroversion of the genital structures was doubtlessly taking place. At first, all genital structures were completely obscured from view; but within a minute's time, both animals began to relax in opposite directions and ultimately to a distance of a good half inch. It could be seen then that there was reciprocal concurrent copulation taking place; for in each case the extended intromittent organ of one was clearly entering the pronounced vaginal opening on the evaginated genital atrium of the other. Mohr (1935) shows a somewhat dark illustration of a copulating pair of *A. fulica* in just this stage.

[1] Also known as egersidium, Reizkörper and Reizorgan.

A great deal of clear slime had been secreted by "A" over the right side of its body, posterior to the genital region, though "C" did not show this. After fifteen minutes, the two individuals had withdrawn considerably and the intromittent organs were obviously being pulled upon. Nothing but the gripping action of the thick basal vaginal muscle could account for the fact that these intromittent organs were being held in place. "A" began to be active at this time and by another five minutes (twenty minutes after complete union) it was very active — extending its tentacles and moving slightly to one side and then the other. During this time, "C" was completely inactive and lay back on the dorsal surface of its shell. In a few minutes, "A" had quieted down once again. Forty minutes after complete union, "C" finally became slightly active by slowly extending and contracting the tentacles. But by this time, "A" had become completely inactive and had withdrawn all its tentacles. "C" soon took up, in a deliberate fashion the task of cleaning up the slime that had accumulated on the anterior portion of its foot, including the clear drop that the other had deposited there. This it did without disturbing the other or without any noticeable tugging on the genital structures. There were frequent rests from this activity and after a full hour of complete union, the two subsided into complete quiescence with the intromittent organs extended until the more attenuate portions could be seen.

Fearing that there would be a very protracted period of quiescence and fearing that there would be a gradual withdrawal of the intromittent organs without any indication of the function of the various male parts in this extroversion process, the intromittent organ of "C" was quickly cut with the scissors as far basally as possible. This brought about a very rapid, simultaneous withdrawal of the intromittent organ of "A" and the complete drawing in of the head of "C" until only the foot projected from the shell. With the forceps, the amputated intromittent organ was removed from the genital orifice of "A". This is shown in lateral and dorsal views in Figs. 52 and 53, respectively.

Very soon, "A" began busying itself with removing the thick mass of slime that it had secreted on its right side. This it rasped at until it was nearly gone and then proceeded to wander about the terrarium. The actions of "C" were quite different. It started several times to crawl but each time it retracted violently, reflecting the reaction to the amputation. In fact the retraction was so sudden that air passed through the pulmonary orifice, or pneumostome, rapidly enough to produce a pronounced squeaking sound. This phenomenon has been observed by Gammon (1943, p. 178) in the so-called "singing snail", *Helix aperta*. In about ten minutes, however, it moved off perfectly

naturally and rasped at a piece of carrot. Later it crawled on "A" and finished up a small stringy mass of slime that "A" had missed. As observed in many other snail groups, there seemed to be a very definite taste for this slime secreted prior to and during copulation. Both snails continued to crawl about more or less together and occasionally rasped at bits of slime on the shell or foot of the other. Even an hour later, "C" showed very intense reaction to the slightest jarring and would pull back into its shell as quickly as if it had been touched with an open flame. The rest, including "A", did not respond to this type of stimulus.

The following morning, "C" was killed and its reproductive tract examined to determine what parts had been amputated as the intromittent organ. As seen in Fig. 50, all but the most apical portion of the penis had been removed as had the basal third of the penial sheath, the entire penial prepuce and a small portion of the apical genital atrium. Next, the intromittent organ was dissected to determine the relationships of these amputated parts (Fig. 51). A re-examination of Figs. 11 and 41 and a comparison of them with Fig. 51 will assist in understanding the confusing reversal of relationships in the extroversion process. This process is initiated by the evagination of the genital atrium (GA) and the penial prepuce (PC) to form the stimulatory organ. This brings the basal portion of the penis proper (BP) to the very tip of the evaginated prepuce. The constriction between these two structures probably prevents further initial eversion. When complete union is effected, there doubtlessly is a contraction of the muscle bands (MB) connecting the sheath (PS) and the prepuce, which pulls the muscular sheath out into the evaginated prepuce. At the same time, there is a complete evagination of the swollen basal portion of the penis (BP) as well as a good share of the very slender middle portion (MP) of the penis. This latter, then is responsible for the very attenuate tip of the intromittent organ. The eversion of these structures pulls the apical portion of the penis (AP) into the intromittent organ. This, of course, becomes very attenuate especially with the squeezing effect produced by the extended basal portion of the sheath. This is further attested to by the fact that it is greatly contracted in the amputated intromittent organ. Since it is a highly muscular structure and was found to be filled with spermatozoa, it is presumed that it has an ejaculatory function. Normally, when the penial retractor (PR) contracts, all these structures are pulled back into the body in their original positions as they are all attached in series. In this case, however, its violent contraction succeeded only in pulling what was left of the apical penis apically right out of the sheath (Fig. 50).

During copulation, no such pronounced "glans" structure could be seen; instead, the intromittent organ seemed very attenuate. This is probably explained by the fact that there was not only a general contraction of the muscular tissue in the intromittent organ at amputation, but the sheath muscle bands (MB) contracted to such an extent that the prepuce wall (PC) became bunched up adjacent to the genital atrial wall (GA, Fig. 51). And even this latter contracted and was pulled distally by the contracting prepuce considerably beyond the level at which it was cut. As Fig. 51 is examined, then, it should be borne in mind that the cut surfaces of the apical penis, genital atrium and penis sheath were originally at the same level and the entire assemblage was much more attenuate.

In general, and as indicated specifically in the anatomy of *Arch. degneri*, probably the contraction of a circular muscle band in the basal portion of the free oviduct insures the insertion of the intromittent organ into the spermathecal duct. The entire length of the vas deferens was inspected and several white sperm masses were found. There was no evidence of spermatophore formation. Only a small amount of seminal fluid was found in the spermatheca.

One interesting factor in this copulation is that two different subspecies from two completely separated localities were sexually compatible. Several instances of the pre-copulatory behavior were noticed in the specimens of *A. iredalei* and they were characteristically the same as observed in this case. These observations, then, probably are typical for the group.

The absence of a thick sheath and the presence of a verge set up still a different problem in *Limicolaria* and *Limicolariopsis*. It is most probable that in these genera the penis proper does not evaginate. Instead, the prepuce must evaginate so as to bring the verge or penis papilla into terminal position. The penis and its thin-walled sheath would then give support to the prepuce to form a substantial intromittent organ.

Webb (1942, etc.) has done a great deal of work on the anatomy of the extroverted copulatory organs in several North American genera and has made some exceedingly interesting and significant observations. He regularly plunges the copulating pair into boiling water to secure the genitalia in the extended condition. With such large animals as the achatinas, however, a more drastic measure had to be taken. If one is seized with a profound conviction that mayhem has been committed, it might help to know that the North American giant land slugs of the genus *Ariolimax* practice auto-amputation of the intromittent organ, or apophallation, as a regular, but not too fitting, culmination to copulation (Mead, 1943).

GENITAL PHYSIOLOGY

During the course of the present study, there have been examined a great number of specimens, varying considerably in form, size and maturity. Many of the observations made, reflect on the very complex interrelationships of the male and female conduits and the function of their component parts. Though a number of these will need rechecking by way of carefully controlled physiological experimentation or histological examination, it seems advisable here to indicate what has been found and what the apparent function, relationships and implications are so that the way might be pointed toward further research along these lines.

As has been pointed out above, it seems perfectly clear that the basal portion of the ovotestis duct, or hermaphroditic duct, acts as a seminal vesicle. It has been found crammed with spermatozoa in every case where the genital system was mature and functioning. There was no exception even in those specimens found in the midst of producing eggs. The question of autofertilization or the existence of some incompatibility factor is immediately suggested. It might be mentioned here that the author has research in progress which should give the answers to this problem.

The talon in general has long been considered a sort of fertilization chamber or "Befruchtungstasche." There is absolutely no evidence in this group of its being anything more than a diverticulum, or caecum, of the ovotestis duct. It frequently contains a mass of spermatozoa which is confluent with that in the ovotestis duct.

Apically, the male and female conduits are intimately associated as will be seen in the examination of the diagram of the spermoviduct in cross section (Fig. 47). The male conduit (♂) is poorly set off from the female conduit (♀) by two unequal, whitish, overlapping walls. These, in turn, are overlapped by an adjacent small portion of the uterine wall which seems to consist of the same type of whitish, firm tissue. The rest of the uterine wall is of softer consistency and cream-colored in the apical uterus and butter-yellow or ochre-colored in the basal uterus. The lumen of the uterine portion of the oviduct is lunate in the individual that is not gravid. This seems attributable to the fact that the voluminous, cream-yellow, compound prostatic acini (PA) are tucked deeply into the infolded portion of the uterine wall and are held in place by connective tissue. The compound acini open basally between the two walls of the male conduit through conspicuous, slightly raised pores (Fig. 45). This whole assemblage, plus a branch of the genital artery (G), is suspended from the diaphragm by a very thin sheet of mesentery (M).

In one of the specimens of *A. iredalei*, which had been killed by plunging in boiling water, there were found high up in the apical uterus five firm, coagulated albuminous masses which were approximately 6 mm. in diameter. These were perfectly homogeneous and contained no sign of an outer calcareous layer. Both these and the very large albumen gland were approximately of the same consistency and color. It is apparent, then, that the ova at this stage were being surrounded by albumen from the albumen gland and were being temporarily stored in the apical uterus. The basal uterus looked perfectly normal.

A gravid specimen of *A. fulica hamillei*, treated in the same way, was found to be in a later stage of egg formation. Both apical and basal portions of the uterus were crammed with 292 thick-shelled, butter-yellow eggs approximately 4x5 mm. When these were removed and the uterine wall was examined, it was found that a portion of the wall adjacent to the male conduit was thrown up into two very irregular longitudinal folds (Fig. 48, F, F) which contained numerous secondary folds. The arrangement of these was such that nearly every egg was somewhere in contact with the uterine wall or its proliferations. The eggs in the apical uterus were just as completely formed as were those in the basal portion. It seems quite apparent that this modification in the uterine wall greatly increases the surface of the shell depositing tissue. The presence of a smooth, even, calcareous covering of the eggs doubtlessly rests in the fact that the eggs are moved about in the uterus during the process of shell deposition — quite after the manner of sugar-coating pills. It is possible that the cream-colored apical uterus lays down the inner pale layers of the shell whereas the butter-yellow basal uterus lays down the outer, butter-yellow shelly layer. One of the eggs was broken open and the embryo within was found to be completely formed and apparently ready to hatch. This near-ovoviviparity is probably attributable to the fact that the snail was held in prolonged conditions unfavorable for oviposition thus forcing a retention of the eggs. As a matter of fact, in response to these unfavorable conditions, the snail had formed a rather thick epiphragm at the time it was killed.

The author has examined specimens of *A. achatina, fulica hamillei, fulica fulica* and *Limicolaria flammea* that contained well-formed eggs. These and probably most other achatinines are oviparous. Ovoviviparity was suspected in one or two species of *Limicolaria* (Robson, 1912). Its sporadic appearance suggests that it has arisen independently several times. The two obvious elements of greater survival value rest in the economy of lime and in the greater protection afforded by prolonged retention in the uterus. The very thin, transparent membrane that covered the embryos of *A. zanzibarica* did not

pass over the aperture of the shell and there was fair evidence that intra-uterine feeding on a mucoid secretion had been taking place. This obviously is a point that needs further investigation.

One thing that was abundantly apparent in this study is that the size of the so-called prostate gland is all out of keeping with its presumed prostatic function, as only a small amount of mucoid fluid accompanies the spermatozoa during copulation. The only other function that could be ascribed to it would be the production of some substance during egg formation, egg laying, or retention of the embryos. When the uterus is full of eggs, the two walls that delimit the male conduit are pulled so far apart that the male and female conduits are completely confluent (Fig. 48). At that time, the pores between these two walls (Fig. 45) face into the lumen of the uterus. Thus it is physically possible for the prostate gland to have a role, for example, of pouring out the large amount of mucus that accompanies egg laying; or to have some similar function in addition to a prostatic function. Apropos of this, there still remains unknown the source of the clear, yellowish drop of fluid that appeared at the tip of the stimulatory organs immediately prior to physical union in copulation (*vide supra*).

At the very apex of the vas deferens, that is, just before it joins the free oviduct, there is a pronounced swelling and, in the freshly killed specimen, a change in color from a pale cream to a light gray-tan or purplish. This swelling was found especially pronounced in the examined specimens of *Limicolaria*. At first, it was thought this was a glandular structure as it seemed to be made up of barely distinguishable acini (*Cf.* Figs. 21, 43). On cutting open several, however, it was found that they were not excessively glandular. Instead, in each case the lumen was found to be quite large and the thin walls densely covered with deep, branching and anastomosing rugae. Sperm was often found present and packed deeply between the rugae, hence giving this structure an external appearance of being an aciniform gland. In the specimen of *A. fulica hamillei*, discussed above, which had been killed shortly after copulation, this structure was found jammed with sperm. From these observations, it would appear that this enlarged region of the vas deferens possibly functions as a sort of subsidiary seminal vesicle. A relay ejaculatory function should be considered.

Frequently there is encountered in the spermatheca a pinkish viscous substance that gives every appearance of being a polysaccharide. Investigations are in progress in related gastropods to determine the exact nature and function of this. It is very possible that it is a nutritive substance desquamated from the spermathecal lining and that it sustains the life and viability of the otherwise short-lived spermatozoa.

Direct and indirect evidence of protandry and seasonally imposed periods of genital atrophy have been found in a number of specimens.

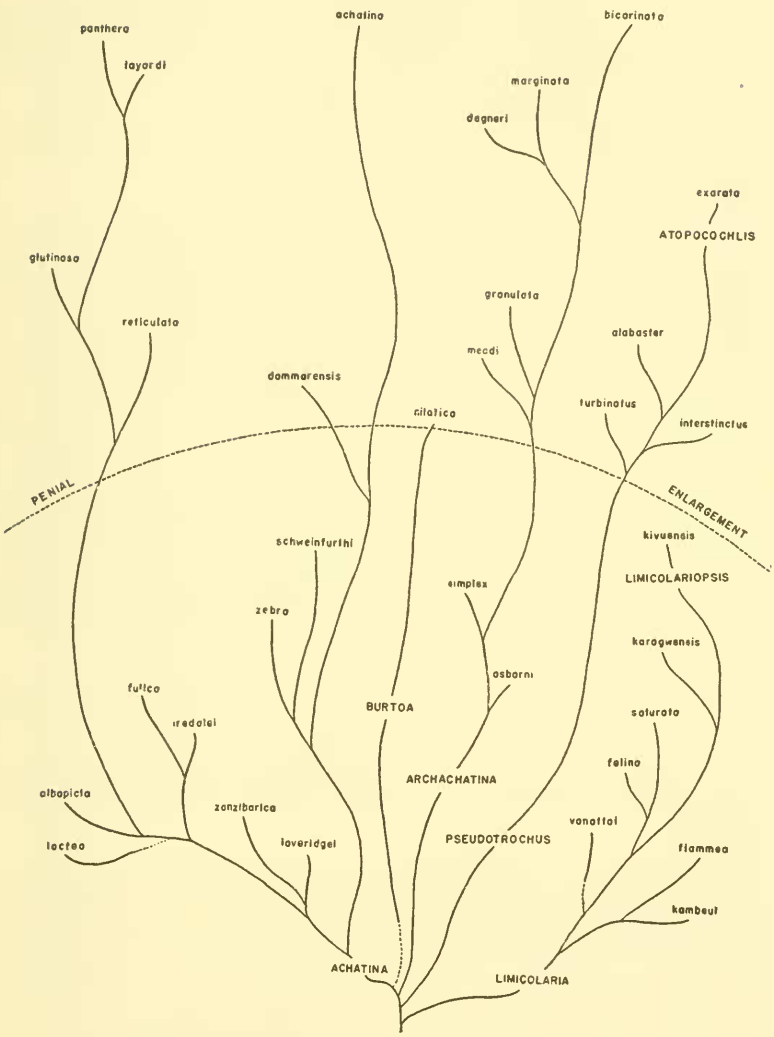
CONCLUSIONS

In spite of the fact that a great number of specimens and a good many achatinid species and subspecies have been examined during the course of this study, they represent only a small portion of what should be examined before any real conclusions or broad generalizations can be safely made. Nonetheless, at this time it is possible to indicate certain obvious trends, affinities, correlations and other factors of phylogenetic significance which should elucidate considerably this whole subject and point the way toward further investigation. Even though subsequent findings may prove to be at variance with the interpretations and provisional conclusions reached in this paper, the effect probably will be largely one of reorientation rather than an actual changing of the fundamental ideas involved. Besides, any means, such as phylogeny, that tends to pull together and put sense into an otherwise meaningless jumble of variously related species is a step in the right direction in clarifying the issue so that eventually the real truth might be reached.

Let us re-examine, then, the several illustrated species with the thought of homology, and therefore phylogeny, foremost in mind. To depict graphically the relationships indicated, there has been prepared a phylogenetic tree of the anatomically known achatinines (Text Fig. 1).

Achatina zanzibarica and *loveridgei* possess proportionately the most diminutive penes of all those examined and despite the fact that Bequaert (1950) has put them in separate subgenera on the basis of shell characters, their genitalia are remarkably similar. The genitalia of *A. iredalei* and *fulica* are of this same general type though the penes are less tripartite and tend to become more elongate. The specimens of *fulica* were especially variable in this latter character. In *A. albopicta*, the genitalia have not departed from this same type though the basal structures have become exceedingly muscular. In each species of this group of five, the basal vagina is short, muscular and cormoid in form. The apical vagina, on the other hand, is short, tubular, and unmodified but indicates a tendency toward greater elongation.

Because of the similarity in shells, it might be presumed that *A. reticulata* is an overgrown version of *albopicta*. The genitalia, however, indicate marked differences. The penis of *reticulata* has become quite robust and so elongate that it projects considerably beyond the apical limits of the sheath. Though there is a very slight enlargement in the



Text Fig. 1 Outline of the phylogenic relationships of the anatomically known Achatininae. For *karagwensis* read *ussuwiensis*.

basal region of the vagina, it is not cormoid nor is the wall thicker than the rest. The genitalia of *glutinosa* seem to have carried this general attenuation still further with a concomitant reduction in

thickness of the sheath. This trend is culminated in *A. layardi* and *panthera,* as the penis is extremely slender and forms, with a small portion of the basal vas deferens, a pronounced loop apical to the sheath. The immature paratypic specimens of *layardi* showed in the basal vagina no tendency toward the formation of the striking sinuations so evident in *panthera.* Along with this development of the vagina in *panthera,* there has been a reduction in the length of the spermathecal duct and free oviduct.

Quite another line of evolution within the genus *Achatina* seems to have taken place in *zebra, schweinfurthi, dammarensis* and *achatina,* which Bequaert (1950) has put in the subgenus *Achatina.* Only the latter species has been examined by the author. It represents an advanced stage in the development of greatly enlarged basal genitalia. The illustrations in the literature of the other three species, which have been reproduced in this work, suggest that this trend may have started with the enlargement of the penis while it was still confined to the thin-walled sheath. This is in contrast to the first group wherein the penis was reduced and the sheath was considerably thickened. However, the greatly elongated vagina, along with the shortened spermathecal duct and free oviduct, in *dammarensis* and *achatina,* indicates either convergent evolution or affinities in the direction of *panthera.* To determine this for certain, it will take a re-examination of *schweinfurthi, zebra* and others in this group, which unfortunately has not been possible.

Robson (1921) indicates sufficient anatomical difference between the subspecies *obesa* and *fulgurata* of *A. zebra* so that their presumed subspecific status is immediately open to question. This is especially the case when it is recalled that no tangible anatomical character of subspecific value has been found in any other examined group of subspecies.

Specimens of *Burtoa nilotica* could not be secured for examination, but the illustrations of the genitalia in the literature suggest that it has arisen from brachyphallate stock close to the stem of the typical *Achatina* as did probably the more primitive members of the genus *Archachatina.* Again, in this latter genus, progressive enlargement of the penis seems to have taken place, for the penis in *osborni afromontana* and *simplex crawfordi* are enlarged, though confined to the short sheath; in *meadi* and *granulata* it projects with the basal vas deferens a short ways beyond the sheath; in *degneri* and *marginata* it is more robust and projects still further; and finally in *bicarinata* it projects as far but has become extremely massive. Of all the achatinids studied anatomically so far, *Arch. simplex crawfordi* is unique in that it possesses a peculiar subterminal partial evagination of the penis.

The genus *Pseudotrochus* also seems to have arisen from stock that had the penis completely ensheathed as indicated in the gravid specimen of *P. turbinatus mucidus* (Fig. 43). It will be recalled, however, that one other fully mature specimen of this same species (Fig. 46) had a basally placed sheath as did the single immature specimen of *P. interstinctus insignis* and the illustrated specimen of *P. alabaster* (Fig. 62). A trend toward an enlargement of the penis beyond the upper limits of the sheath seems therefore to be in progress. The illustration of the genitalia of *Atopocochlis exarata* indicates that this species and the examined species of *Pseudotrochus* are apparently quite closely related thus supporting the contention in some quarters that all these are congeneric. The very elongate vagina and the abbreviated free oviduct and spermathecal duct in this group are reminiscent of the condition in *A. achatina* and *panthera*.

The evolution of the genus *Limicolaria* has been quite distinct as indicated by the fact that the species illustrated in this paper are in agreement with each other, and distinguished from all other achatinids examined, in the following characters: the formation of a definite verge through no addition of new structures but merely through changed relationships of those already present, a great development of the muscle tissue in the penis proper, larger and fewer prostate gland acini, and a large spermatheca with both apical and basal swellings. Further, they all have in common a vas deferens that does not reach the peniovaginal angle and a vagina that is long and unmodified.

The retention of a fairly large lumen in the penis proper, the development of a long penial prepuce which makes the penial sheath appear apically placed, and a vagina that is shorter than the penis plus its prepuce, set off *L. kambeul* and *flammea* from the others. A development of a loose spongy mass of tissue by the walls of the penis proper with a concomitant reduction of the penial lumen to a narrow canal equivalent to that of the vas deferens, the retention of a fairly short penial prepuce, the enlargement of the verge, and the presence of a vagina longer than the penis plus its prepuce, characterize *L. saturata*, *felina* and *ussuwiensis*. *L. vanattai* unfortunately has not been shown in sufficient detail by Pilsbry to make it possible to determine what its real affinities are in the genus. The apparently clavate spermatheca is in contrast with the other examined species. Pilsbry's assumption that a diaphragmatic insertion of the penial retractor is typical in this genus is no longer tenable. *Limicolariopsis kivuensis* is so strikingly like the latter group of *Limicolaria* species that one might well question the reason for its being placed in a different genus. Actually, these are more similar than the two groups of *Limicolaria* are to each

other. The examination of the genitalia of other species of *Limicolariopsis* should prove enlightening as would a much needed detailed anatomical study of the large and confused genus *Limicolaria* which will never be in taxonomically sound status until this is done.

To sum up then, the present study has revealed convincing indication that there are in *Achatina*, *Archachatina* and *Pseudotrochus* strong tendencies toward the maintenance of a simple tubular penis, the enlargement of it, and finally the extension of it beyond the sheath with a concomitant almost complete reduction of the prepuce. In *Limicolaria*, on the other hand, the tendencies seem to be directed toward the formation of a verge, elongation of the prepuce and reduction of the penis proper to a thick mass of muscle fibers through the hypertrophy of the middle muscle layer.

The whole worth of a study of this sort depends not only upon anatomical variability, but variability of a tangible and significant nature. The real problem, therefore, rests first in discerning the presence of variability and then determining its nature. It is only after a good many dissections that a concept of this latter begins to emerge. The factors responsible for and influencing the expression of variability in this group should be examined at this time.

First of all, individual differences are ever present and confuse the picture, especially when too small a sample is taken. The talon, for example, is always present but varies greatly from specimen to specimen. The type of insertion of the penial retractor, as shown above, is also a highly variable and undependable factor and is therefore taxonomically valueless; though there is some indication that it may prove constant enough to be a helpful character in the identification of some species. Another factor is the degree of maturity. This greatly influences the expression and relationships of the anatomical characters in the genitalia. For this reason, the nature of the albumen gland can never be used for more than determining the degree of maturity and in some cases determining whether eggs are soon to be formed or have just been formed. In very immature specimens, the genitalia are of small caliber and tend to be strongly attenuated and quite translucent. Immature specimens of several species that normally have the penes completely ensheathed in the adult animal (*e.g. Arch. osborni afromontana*), were found with the penis projecting atypically well beyond the sheath. In somewhat more mature specimens, protandry, which seems to be universal in this group, adds its bit of confusion. The possibility of genital atrophy, imposed by seasonal changes, must also always be considered. In such cases, the genitalia lack the attenuate nature of those in the immature specimen, are proportionately reduced in caliber, and retain the coloration and opaque-

ness of the mature system. Specimens of *A. fulica* from Saipan and the Palau Islands rather clearly demonstrated this phenomenon. One thing is certain though, large immature specimens can be distinguished anatomically from small mature specimens. This is not always possible in the study of the shell alone, as witnessed by the fact that in the past immature and adult individuals of the same species have been described as specifically distinct.

As explained in the introduction, killing by any method will produce at least some distortion through contraction. For this reason, the length of the penial retractor is usually a very variable factor and therefore not a dependable one; however, in some species it is found quite consistently very short or very long. A similar variable degree of contractility in the vas deferens will determine how closely this structure will approach the peniovaginal angle. Severe contraction in the penis may cause it to rest in a reverse direction or become acutely angulate as, for example, shown in Pilsbry's illustration (1904–05, pl. 65, Fig. 42) of *L. vanattai*. Such cases must be distinguished from cases of natural angulation such as found in *L. flammea*.

The most tangible and constant specific, and to some extent generic, anatomical variations are found in the basal genital structures, and especially in the penis and its sheath. Before we seek an explanation for this, let us examine some of these variations or modifications.

As in any other evolving group, various combinations of characters are tried and often carried to extremes. Gigantism has always been a popular variation and it has been independently attempted in the genitalia of this group, by way of penial enlargement, several times. This, then, introduces an element of convergent evolution which invariably complicates interpretation. All the evidence indicates that penial enlargement is an experimentation in this group and is not a prototypic feature. Attenuation of the penis is another trend that has been tried, often concurrently with penial enlargement. Myopachynsis or muscle hypertrophy has been tried in the basal vagina of *A. fulica*, and closely related species, and in the penial sheath of *A. albopicta* as a still different type of variation. And as a final main type of variation found in the examined species, verge formation with attendant penial alterations has been undertaken by *Limicolaria* and *Limicolariopsis*. Some of these variations have initially taken place within the confines of the penial sheath and for this reason, brachyphallate species of wholly different stocks tend to look superficially very much alike until the penes are exposed.

A profound question is immediately apparent. Why is it that variations and modifications in the internal anatomy have been limited almost entirely to the basal genital structures and especially to the

penis and its sheath? An attempt to answer this cannot be made without indulging in dangerous speculation. Nonetheless, what seems to the author to be a plausible explanation is given here. The intromittent organ, which is formed often in a complex manner by the penis, the prepuce and the sheath, is the only internal structure that comes in direct contact with the external environment. Any variation in the form of the intromittent organ, such as would be caused if the proportions of its components were altered, might introduce an element of physical incompatibility with the receiving components of the female genital tract. There would thus be a premium of survival value put on the effecting of reciprocal changes in the complementary form of the female tract. A series of such variations and reciprocal changes in a given stock could lead to a definite trend that might eventually be culminated in a very exaggerated condition in certain structures. It is not a mere coincidence that the vaginae of the dolichophallate *A. panthera* and *achatina* are very long or that the basal vagina of *A. reticulata* has lost the cormoid proportions possessed by the closely related brachyphallate *A. albopicta* or that both penis and vagina are short in *Arch. osborni afromontana* and *Arch. simplex crawfordi*.

To hypothecate a strange, greater natural stability in all internal structures except the basal genitalia is but to beg the question. The basal genitalia have, because of copulation between different individuals, structural interrelationships of a variable nature not found between any of the other internal structures. The radula is the only other internal structure that can begin to approach this nature and it is notoriously a variable structure in most groups.

Of all the species examined, *A. fulica* proved to be genitally the most variable. This fact might be interpreted as an index of a general, basic genetic instability which could explain the great adaptability this species has demonstrated in the many different types of environments into which it has been introduced in the past hundred years.

Finally, the author wishes to make perfectly clear that it is not his intention to propose or even suggest that the achatinid genital characters should take precedence over those contained in the shell but, rather, that the two be used together to construct a sound classification in this confused group. In the past, the use of the shell characters alone, in most cases by sheer necessity, has been far from satisfactory as altogether too frequently such characters have proven to be intangible, over-lapping variations in degree of color, size, shape or sculpture. It has been shown in this study that many rather minor shell characters can be given real significance when they are backed by tangible differences in the genitalia. With the correlation once established, these minor shell characters are then used with confidence

in the absence of, or when it is not practicable or desirable to examine, the soft parts. As an example, a comparison at first of the very similar reticulately sculptured shells of *A. albopicta* and *reticulata* indicated no more than a subspecific difference between the two. An examination of the genitalia, however, revealed striking differences which most certainly were of specific caliber. On the strength of these differences alone, the two were set up as distinct species.

Cummings and Robson (1914) suggested in their short article that internal structures would probably be found to be of generic and ordinal value, whereas the external structures would be more valuable in determining specific and varietal differences. This belief was later retracted by Robson (1921) with the statement, "There would now be grounds for considering that the internal anatomy is neither more nor less variable than the external structures." In the light of the present study, neither the original suggestion nor its retraction leave what is believed to be the correct implications. Actually, a great deal of evidence has been brought forth in support of the contention that the genital characters are not only helpful but often indispensable in determining species and higher categories. Further, they have been shown to hold forth the only hope of determining the exact status of some of the apparently bastard genera in this family whose present status is based solely upon shell characters. On the other hand, this study has shown that the lower categories, in probably every case, must be determined entirely upon the basis of shell characters as witnessed, for example, by the condition in the three examined, anatomically indistinguishable subspecies of *A. fulica*.

Once again then, both conchological and anatomical data are required and their differences must be reconciled in order to put the Achatinidae in sound taxonomic status. But this cannot be realized until a great deal more anatomical data have been gathered. That is the immediate need in this problem.

BIBLIOGRAPHY

Bacci, G.

1939. Spedizione Zoologica del Marchese Saverio Patrizi nel Basso Giuba e nell'Oltregiuba. Molluschi. Ann. Mus. Civ. Stor. Nat. Genova, **58**, pp. 333–338, 2 figs.

Baker, H. B.

1939. A Revision of *Spiraxis* C. B. Adams. Nautilus, **53**, pt. 1, pp. 8–16, Pls. 3–5.

Bequaert, J. C.

1950. Studies in the Achatininae, a Group of African Land Snails. Bull. Mus. Comp. Zoöl., **105**, pp. 3–215, Pls. 1–81.

Bequaert, J. C. and W. J. Clench

1934. Studies of African Land and Fresh-Water Mollusks. 3. West African *Achatinae* Related to *Achatina balteata* Reeve. Amer. Mus. Novitates, No. **705**, pp. 1–16, 7 figs.

1936. Studies of African Land and Fresh-Water Mollusks. VII. A Revision of the Genus *Archachatina* Albers. Rev. Zool. Bot. Afric., Brussels, **29**, pt. 1, pp. 73–96, Pls. 1–2.

Boettger, C. R.

1939. Bemerkungen über die in Deutschland Vorkommenden Bernsteinschnecken (Fam. Succineidae). Zool. Anz., **127**, pts. 3–4, pp. 49–64, 17 figs.

Brancsik, Karl

1893. *Achatina mossambica* sp. nova. In: P. Frey, Die Insel Moçambique und ein Ausflug nach dem Nächtsliegenden Festland. Jahresh. Naturw. Ver. Trencséner Comit., **15–16**, (1892–1893), pp. 116–117, Pl. 6, Figs. 2, 2*a*, 2*b*.

Clench, William J. and Allan F. Archer

1930. New Land Snails from Tanganyika Territory. Occ. Pap. Boston Soc. Nat. Hist., **5**, pp. 295–300, 3 figs., 1 Pl.

Connolly, M.

1925. The Non-Marine Mollusca of Portuguese East Africa. Trans. R. Soc. South Africa, **12**, pt. 3, pp. 105–220, Pls. 4–8.

1939. A Monographic Survey of South African Non-Marine Mollusca. Ann. South Afr. Mus., **33**, pp. 1–660, 58 figs., Pls. 1–19.

[Cummings, B. F. and G. C. Robson] (as "X")

1914. Taxonomy and Evolution. Amer. Naturalist, **48**, p. 369.

Degner, E.

1922. Mollusca. In: W. Michaelsen, Beiträge zur Kenntnis der Land- und Süsswasserfauna Deutsch-Südwestafrikas. (Hamburg), **2**, pt. 1, pp. 1–52.

DESHAYES, G. P.
1851. In: Férussac, Histoire Naturelle Générale et Particulière des Mollusques Terrestres et Fluviatiles. (Paris), **2**, pp. 154–155; Atlas, Pls. 127A (colored), 127B (colored), and 127A-127B (one uncolored Plate), and Expl. of Plates, pp. 18–19

FURTADO, ARRUDA
1888. Sur le *Bulimus exaratus* Müller. Journ. de Conchyl., **36**, pp. 5–10, Pls. 2–3.

GAMMON, EARLE T.
1943. Helicid Snails in California. Bull. State California Dept. Agric., **32**, pt. 3, pp. 173–187.

GERMAIN, L.
1933. Mollusques Terrestres et Fluviatiles de l'Afrique Occidentale Française. Bull. Comité Etudes Hist. Sci. Afrique Occidentale Française, **16**, pt. 2, pp. 169–236, figs.

HOFFMANN, H.
1922. Ueber die Entwicklung der Geschlechtsorgane bei *Limax maximus* L. Zeitschr. Wiss. Zool., **119**, pp. 493–538.

IHERING, H. VON
1892. Morphologie und Systematik des Genitalapparates von *Helix*. Zeitschr. Wiss. Zool., **54**, pp. 386–520, Pls. 18–19.

KEFERSTEIN, WILHELM
1862–1866. Die Weichthiere (Malacozoa). In: Bronn's Classen u. Ordnungen des Thier-Reichs. (Leipzig and Heidelberg), **3**, pt. 2, pp. 523–1500, 136 figs., Pls. 45–136.

LANG, ARNOLD
1900. Lehrbuch der Vergleichenden Anatomie der Wirbellosen Thiere. Mollusca. (Jena).

LEHMANN
1864. Untersuchung Einiger Schneckenthiere. Malak. Blätt., **11**, p. 48, Pl. 1, fig. 3.

MARTENS, E. VON and F. WIEGMANN
1898. Land- und Süsswasser-Mollusken der Seychellen. Mitt. Zool. Samml. Mus. Naturk. Berlin, **1**, pp. 1–96, Pls. 1–4.

MEAD, ALBERT R.
1943. Revision of the Giant West Coast Land Slugs of the Genus, *Ariolimax* Mörch. (Pulmonata: Arionidae). Amer. Midl. Nat. **30**, pt. 3, pp. 675–717, 25 figs., map, 4 Pls.

MEISENHEIMER, JOHANNES
1912. Die Weinbergschnecke *Helix pomatia* L. Monographien Einheimischer Tiere, (Leipzig), **4**, 140 pp., 72 figs., 1 Pl.

Melvill, J. C. and J. H. Ponsonby
1898. A Contribution Towards a Check-List of the Non-Marine Molluscan Fauna of South Africa. Proc. Malac. Soc. London, **3**, pp. 166–184.

Mohr, J. C. van der Meer
1935. Eine Wanderlustige Schnecke: *Achatina fulica* Fér. Natur u. Volk, Frankfort a. M., **65**, pt. 2, pp. 62–67, 8 figs.

Odhner, Nils Hj.
1932. New or Little Known African Land Shells. Proc. Malac. Soc. London, **20**, pt. 1, pp. 19–40, 33 figs., 1 Pl.

Pilsbry, Henry A.
1904. Family Achatinidae. In: G. W. Tryon, Jr. and H. A. Pilsbry, Manual of Conchology, **16**, pp. 205–329, Pls. 1–37.
1904–1905. Family Achatinidae. *Op. cit.*, **17**, pp. i–xviii and 1–232, Pls. 1–65.
1919. A Review of the Land Mollusks of the Belgian Congo Chiefly Based on the Collections of the American Museum Congo Expedition, 1909–1915. Bull. Amer. Mus. Nat. Hist., **50**, pp. 1–370, Pls. 1–23.

Pilsbry, Henry A. and J. Bequaert
1927. The Aquatic Mollusks of the Belgian Congo. With a Geographical and Ecological Account of Congo Malacology. Bull. Amer. Mus. Nat. Hist., **53**, pt. 2, pp. 69–602, 94 figs., 15 maps, 77 Pls.

Pollonera, Carlo
1909. Molluschi. Stylommatophora. Spedizione al Ruwenzori di S. A. R. il Principe L. Amedeo di Savoia, Parte Scientifica. (Milano), **1**, pp. 181–205, 5 Pls.

Quoy, J. R. C. and J. P. Gaimard
1832–1834. Zoologie. In: Voyage de . . . l'Astrolabe . . . pendant . . . 1826–29, sous le Commandement de M. J. Dumont d'Urville . . . (Paris), **2**, pp. 152–155. Atlas, Pl. 49, fig. 21; Explanation of Plates in **3**, pp. 879–880.

Reynell, Alexander
1906. On *Burtoa nilotica* (Pfeiffer) and its Relationship to *Achatina*, etc. Proc. Malac. Soc. London, **7**, pt. 3, pp. 197–200, Pl. 17, fig. 2*a*, *b*, *c*.

Robson, G. C.
1912. On a Case of Presumed Viviparity in *Limicolaria*. Proc. Malac. Soc. London, **10**, pp. 32–33.
1921. On the Molluscan Genus *Cochlitoma* and its Anatomy, with Remarks upon the Variation of Two Closely Allied Forms. Proc. Zool. Soc. London, pp. 249–266.

Schmidt, Adolf
1855. Geschlechtsapparat der Stylommatophoren in Taxonomischer Hinsicht. (Berlin), 52 pp., 14 Pls.

Semper, C.
1874. Reisen im Archipel der Philippinen. II. Wissenschaftliche Resultate. Landmollusken. (Wiesbaden), **3**, pp. 142–146, Pl. 12, figs. 1–3, 17, 22.

Simpson, George B.
1901. Anatomy and Physiology of *Polygyra albolabris* and *Limax maximus* and Embryology of *Limax maximus*. Bull. New York State Mus., **8**, pt. 40, pp. 241–314, 28 Pls.

Simroth, H. and H. Hoffmann
1908–1928. Mollusca (Weichtiere). In: Bronn's Klassen u. Ordnungen des Tier-Reichs. (Leipzig), Bd. **3**, Abt. 2, Buch 2: Pulmonata, pp. i–xvi and 1–1354.

Taylor, John W.
1894. Monograph of the Land and Freshwater Mollusca of the British Isles. (Leeds), **1**, Structural and General.

Van Cleave, Harley J. and Jean A. Ross
1947. A Method of Reclaiming Dried Zoological Specimens. Science, **105**, No. 2725, p. 318.

Watson, Hugh
1928. The Affinities of *Cecilioides* and *Ferussacia*, Illustrating Adaptive Evolution. Journ. Conch., **18**, pt. 8, pp. 217–243, 11 figs., 2 Pls.
1934. *Natalina* and Other South African Snails. Proc. Malac. Soc. London, **21**, pt. 3, pp. 150–198, figs., Pls. 19–21.

Webb, Glenn R.
1942. Comparative Observations of the Mating Habits of Three California Landsnails. Bull. South. California Acad. Sci., **41**, pt. 2, pp. 102–108, Pl. 25.
1943. The Mating of the Landsnail *Haplotrema concavum* (Say). Amer. Midl. Nat., **30**, pt. 2, pp. 341–345, 5 figs.
1947. The Mating-Anatomy Technique as Applied to Polygyrid Landsnails. Amer. Naturalist, **81**, pp. 134–147.
1947. Studies of the Sex-Organs of Mating Polygyrid Landsnails. Trans. Illinois Acad. Sci., **40**, pp. 218–227, figs. 1, 2.
1948. Comparative Observations on the Mating of Certain Triodopsinae. Nautilus, **61**, pt. 3, pp. 97–103, 4 figs.
1948. The Mating of *Stenotrema fraternum* (Say). Nautilus, **62**, pt. 1, pp. 10–12, 4 figs.